ALLAN FRASER *writes*

The career and character of Dr. A. L. Hagedoorn are adequately sketched in Sir John Hammond's Memoir of that remarkable man: I shall deal only with his book. Just as the man was remarkable, so also is his book. First published in 1939, it was reprinted ten times during Hagedoorn's own lifetime. The Fifth revised edition was published in 1954, the year after his death. This, the Sixth edition, is as he wrote it, except that I have ventured to add short comments to certain chapters. That task has been a rewarding one. It impelled me to re-read yet again a book I have always valued and enjoyed. It increased my admiration of the penetrating grasp, the immense experience, the healthy common sense and the robust good humour which Hagedoorn displays. Again, there is the vivid vitality of his English prose. That a Dutchman should express himself so naturally, clearly and forcibly in another language is in itself a considerable achievement.

I have always been glad that Hagedoorn entitled his book *Animal Breeding* rather than "Animal Genetics" because the practice of Animal Breeding is so very much older than Genetics. The fact is forgotten too often, perhaps even at times forgotten by Hagedoorn himself who, as a trained geneticist, naturally had profound faith in the utility of his science.

He had a sound training in formal genetics although latterly it may well be that the genetics he taught was more reminiscent of Bateson than of Sewall Wright.

He had a profound understanding of the problems and practice of the animal breeder. I doubt whether any scientifically trained person has ever had an understanding equally profound. His extensive travels; his insatiable curiosity and his intimate contacts as a consulting geneticist gave him an insight and a sympathy somewhat lacking in the average geneticist. Hagedoorn really appreciated the business he was anxious to reform. Apart from the Norwegian, Christian Wriedt, there have not been many other geneticists who have done so.

There is no doubt that, whatever its alleged imperfections, this book of Hagedoorn's has done an immense amount of good. It has been very widely read both by students in agriculture and by practical breeders. At the very lowest valuation it must be admitted that, so far as genetics is concerned, Hagedoorn has played the role of a genetical Baptist, making smooth the way of those that come after.

Moreover, to anyone even mildly interested in Animal Breeding, his is a most fascinating book. It contains so much diverse and unique information not to be found elsewhere. It is a book full of personal experience, of anecdote, of human understanding and of profound common sense. It reads easily, like a novel, and is one in which, every now and again, between the more formal presentation of genetical theory, the vitality, wisdom and humour of its author come bubbling through.

Agricultural and Horticultural Series

ANIMAL BREEDING

ANIMAL BREEDING

BY

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Memoir: Dr. A. L. Hagedoorn

Dr. A. L. Hagedoorn obtained his early training in genetics in Holland, the land of his birth. He then went to California, where he obtained his Doctor's degree and continued his work on animal breeding. Afterwards he came back to Europe and joined the noted firm of Vilmorin, the leading seedsmen in France.

He was intensely interested in the application of the science of genetics to animal breeding and in this quest he travelled widely to study the many applications to animals and plants in different parts of the world.

In 1914 he went out to the Dutch East Indies and he came into contact there with many practical problems which the science of genetics could solve.

After returning to California, where he wrote a valuable book on *The Relative Value of the Processes causing Evolution*, and a short period in Germany he came back to Holland and set up as a consulting geneticist both for plant and animal breeders. He became Head of the Department of Genetics at the Institute of Preventive Medicine and lectured at the University of Leyden, became Secretary of the Dutch Genetics Society, and ran his own smallholding just outside Utrecht; this he used for experiments in breeding dogs, poultry and mice. He produced some very good sex-linked breeds of poultry and advised many breeders of ducks and poultry in Holland to their great advantage.

He was an outspoken man and had no hesitation in criticizing established practices of Breed Societies, criticizing them as being "fanciers" rather than breeding for commercial qualities, although at the same time he assisted fanciers with their

problems, for he was very interested in these from the standpoint of evolution. He had a keen sense of humour, could take criticism well and enjoyed an argument.

He paid many visits to this country and did all he could to persuade cattle breeders to adopt the progeny test as the soundest method of breeding for milk production.

In his poultry experiments he developed the nucleus system of breeding as the most practical means of spreading good genetic material throughout the breed. As this was rather similar to the methods of breeding practised by large Merino flock owners in Australia he went out there and discussed this and other matters with them. His work in Australia was greatly appreciated by the station owners, many of whom kept in constant correspondence with him.

From Australia he went on to South Africa in 1949 and then to Southern Rhodesia, where the problem of breeding animals and plants suited to the climatic conditions appealed to him. There he finished his book on *Plant Breeding*. From Southern Rhodesia he went several times to the Union of South Africa to give advice. In this period he contracted an illness which brought him back to Holland. When back there he prepared this new revised edition of his book on *Animal Breeding* which has been an inspiration to many. In addition, he also wrote in collaboration with Geoffrey Sykes a book on *Poultry Breeding*, and continued to advise breeders in many parts of the world.

His criticisms of practical breeding methods and suggestions for their improvement led to much controversy out of which have come many useful ideas for the improvement of livestock.

By his death on 20th November, 1953, at the age of 68 one of the most colourful and progressive figures in animal breeding has been lost.

JOHN HAMMOND

CAMBRIDGE, 1953

Introduction to the First Edition

Man, to be able to exist at all, is dependent upon his domestic animals and cultivated plants. Everything we eat, and everything we wear, with very few exceptions, is the product of cultivated organisms. Between man and his domestic animals and plants exists a relationship that can only be called true symbiosis, for the domestic animals have been so changed from the wild species from which they have descended that they could not exist without man's aid, and the same is true of almost all our cultivated plants.

The breeding of animals is under human control, and the breeders decide which individuals shall produce the next generation. In almost every instance the breeder makes a choice, even if he does not know what causes the differences he observes between his animals. At present we know that there are two fundamentally different sets of causes for variability. Variability may be partly due to differences in the sets of inherited developmental factors, and part of all variability must always be due to differences in environmental influences. As only differences in inherited make-up are inheritable, it is evident that a knowledge of the science of heredity should make it considerably easier to choose intelligently between the many animals from which only a few need be saved for breeding. The fact that the domestication of animals is a very old art, whereas the science of genetics is very new, shows that even without any knowledge of heredity man is able to domesticate animals and improve them. Such progress, however, is very slow and uncertain, and it has been shown that rational and genetically well-founded methods of selection make it possible to proceed with a certainty and a speed that were formerly unthought of.

The co-operation of professional geneticists in plant breeding and animal breeding only dates from about 1910. It so happens that, as a young geneticist, I was called upon to play a rôle in the revolution in plant-breeding methods that started in the beginning of this century. As a result of the close co-operation of the plant-breeding firms and institutes with us geneticists, plant breeding was placed upon a different foundation, and a selection based upon breeding value (genotype) was substituted for the former system of selecting according to personal merit of individual plants (phenotype) or according to qualities thought to be correlated to the one sought.

For different reasons plant breeders have been much more ready than animal breeders to profit by the teachings of our new science, Genetics. In a relatively short time the improvement of plant-breeding technique has been so rapid that round about 1920 the old methods were almost forgotten and plant breeding was definitely changed over. An enormous lot of work still remains to be done, but the principles are very well understood and the planning of new work is only a matter of details.

Animal breeding, however, has lagged behind plant breeding in a way that has become more and more apparent to many of my colleagues. To me it became apparent long ago that some of us should devote some of our energy to doing for animal breeding what we have been doing for plant breeding for such a long time. About 1910 I started to investigate animal-breeding methods, and gradually I have been drawn into this subject more and more, so that in the last fifteen years almost all my time has been spent in co-operating with animal breeders to help them solve their problems.

It has been apparent to me, from the start, that the problems of animal breeding are fundamentally the same as those of the plant breeders. The greatest difficulty has been the fact that the field of study is so enormously great, and that so very few of my colleagues have been interested in animal-breeding problems.

During the last twelve years I have been conducting a bureau of Applied Genetics as secretary of the Dutch Genetic Association, and during those years it has been my good fortune to co-operate with a very great number of breeders, both in Holland and in other countries. In the different countries in which I spent some years of my life—in the United States, in France,

in Germany, in the Dutch Indies—I have always made it a point to study animal-breeding methods and the attempts of my colleagues to introduce similar rational methods such as we have been able to introduce in plant breeding. I have learned quite a lot about animal breeding and especially about the stumbling-blocks that strew the path of the progressive breeder.

In animal breeding there is just now starting the same revolution in methods that was in full activity about 1910 in plant breeding. We are fighting conservatism and ignorance, especially among the men who have been looked up to as authorities in these matters. We have to help the breeders to discard some of the same wasteful and stupid methods that the old school of plant breeding used.

One of the greatest difficulties in the career of a geneticist who wants to co-operate with animal breeders is to learn to hew to the line, let the chips fall where they may. No useful purpose is served in trying to "save the faces" of well-known authorities, when the methods they advise are fundamentally and patently wrong and wasteful. It is much better to have the respect of the honest breeders, striving to improve the quality of their livestock for the benefit of agriculture, even if this means going over the heads of the authorities to reach the farmers.

In meditating upon the necessity of writing a book on animal breeding I have hesitated between a book destined to teach a sufficiency of genetics to animal-breeding authorities, Government men, teachers and herd-book officials, or a book destined for the breeders themselves. Most recent books on animal breeding have been of the former kind. This is true of Crew's book, and also of the excellent book of J. Lush, *Animal Breeding Plans.*

For several reasons I have chosen to write the second kind of book. I am not so optimistic as to believe in the possibility of convincing the conservative, older authorities on animal breeding of the error of their ways, where I think they are fundamentally wrong. In this I am in full agreement with Boutflour, who has repeatedly argued that some of these men are unteachable, because they take the attitude that the old ways will last their time. If we can reach the younger generation and stop them from taking the old wisdom for granted, if we can make them think for themselves, we will certainly get results.

After all, the authorities only hold the opinion they have distilled from the experiences of the breeders, so that if we can

make the breeders accept more rational working methods, the authorities are bound to follow along.

In writing this book directly for the breeders, I follow the example of Christian Wriedt. His little book in Norwegian is just exactly what the breeders want. It was an excellent idea of Punnett to translate it into English. It has just one fault, it is much too small, and for this reason just touches upon some subjects that merit more extensive treatment. If Wriedt had lived, he would have been the right man to write the book that I am now attempting to write.

In the pages that follow I have tried to give the breeders of the different domestic animals enough of the knowledge of genetics to enable them to understand the working of the methods they are using, or those they should use. I have tried to provide an answer to the most likely questions I have learned to anticipate, and in doing this I have endeavoured to avoid the use of scientific terms when plain English would serve equally well. Of course it is impossible to anticipate all questions, and I shall be happy if breeders who read the book will consult me when they are in any difficulty.

In many questions of practical animal breeding it is possible to take either of two wholly different standpoints: (1) a breeder of any kind of animal can rest content when he, as a breeder, makes a profit out of his efforts; or (2) the standpoint can be taken that the ideal in breeding animals is to make the different breeds as profitable as possible from a general economic standpoint. Although I have never forgotten the situation of the breeders, I must confess that my own attitude has been consistently this, that we should aim to make each breed of domestic animals as good as possible to fill its niche in the symbiosis-group in which it exists.

This separation between the personal attitude of the breeder and the general outlook of agriculture in matters of breed improvement is most striking in relation to the herd-books of the larger farm animals, especially those of cattle. Where necessary, I have not hesitated to point out the matters in which the herd-book societies are not now working as well as possible at the amelioration of the breeds they sponsor from an economic standpoint.

If I had written this book five years ago, I would certainly have felt compelled to add some chapters on the statistical side

of genetics. In many chapters I feel that it is somewhat presumptive on my part to ask my readers to accept my views without going into the mathematical proof necessary fully to understand my reasons. If any reader feels this as much as I do, I advise him to take Lush's book on *Animal Breeding Plans*, and to get the necessary statistics from this excellent book.

My book has really grown out of my practical experience in co-operating with breeders, and out of my own activity as a breeder. My experience in animal breeding is the sum of the experience of the men who have co-operated with me in solving their practical difficulties.

In many instances I am advocating what has never been put to the test of practical experience. In this we geneticists have to follow the example of the engineers who dare to plan a building or a bridge that has never been built before.

The most extensive piece of engineering of this kind in the present book is my nucleus scheme of breeding the larger domestic animals. So far no herdbook society is planning to improve a breed along those lines, although I dare to prophesy that it will have to come to it in the near future. One of the reasons why I venture to recommend this scheme with the utmost confidence is that it has been tried out with very great success in poultry and ducks.

I wish to thank Dr. Hammond for suggesting the writing of this book, and I cordially acknowledge the encouragement and help received from several different friends, such as R. Boutflour of the Royal Agricultural College, Cirencester; Mr. Hunter Smith, St. Albans; Dr. Mogens Plum, Copenhagen; Mr. R. van Vloten, Heelsum; and many others.

At the end of this introduction I want to ask the reader's indulgence for having written this book in a foreign language. My own language, Dutch, happens to restrict the book to my own country, its colonies and South Africa, and I like to think that it will be useful to many more breeders when I use English.

A. L. HAGEDOORN

SOESTERBERG, HOLLAND

1939

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List of Illustrations

Diagrams in the text.

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Photographic illustrations between pages 180 and 181.

Publishers' Note

It is seven years since the last revision to this work was undertaken by the late Dr. Hagedoorn, but as the larger part of it was written more than twenty years ago, we have thought it well to have the whole re-examined in the light of later developments in practice. We deemed this advisable mainly in the interests of students amongst whom the book has a continuing and large circulation.

We have been fortunate in obtaining the services of Dr. Allan Fraser to do this work, and he has made all the observations he considers necessary in the form of notes at the end of chapters requiring them.

Chapter One

Introductory

By Dr. ALLAN FRASER

The career and character of Dr. A. L. Hagedoorn are adequately sketched in Sir John Hammond's Memoir of that remarkable man. In this Introductory Chapter, therefore, I shall deal only with his book. Just as the man was remarkable, so also is his book. First published in 1939, it was reprinted ten times during Hagedoorn's own lifetime. The Fifth revised edition was published in 1954, the year after his death. This, the Sixth edition, is as he wrote it, except that I have ventured to add short comments to certain chapters. That task has been a rewarding one. It impelled me to re-read yet again a book I have always valued and enjoyed. It increased my admiration of the penetrating grasp, the immense experience, the healthy common sense and the robust good humour which Hagedoorn displays. Again, there is the vivid vitality of his English prose. That a Dutchman should express himself so naturally, clearly and forcibly in another language is in itself a considerable achievement.

I have always been glad that Hagedoorn entitled his book *Animal Breeding* rather than "Animal Genetics" because the practice of Animal Breeding is so very much older than Genetics. The fact is forgotten, too often forgotten, perhaps even at times forgotten by Hagedoorn himself who, as a trained geneticist, naturally had profound faith in the utility of his science.

That, incidentally, seems to me to be a rather curious feature of Hagedoorn's work—his profound faith in the Mendelian hypothesis combined with the fact—for it is a fact which it is better to acknowledge—that his reputation as a geneticist was never an especially high one among geneticists themselves.

Rather the same curious anomaly might be said to apply to the late Mr. Odlum, the noted breeder of Friesian cattle. Might there not be a certain element of professional snobbery or jealousy in that denigration? Hagedoorn was very successful in his writings, his lectures and his consultations. Odlum sold his bulls at high prices. Certainly, as regards Hagedoorn, some of the criticisms by his fellow geneticists always struck me as being somewhat unfair. Hagedoorn has been accused of the avoidance of quantitative treatment of genetical problems to the extent of dangerous over-simplification. It should not be forgotten, however, that he was, confessedly, writing for the practical breeder and not for the scientific specialist. He had to over-simplify in order to be understood. In genetical language, as in all languages, the alphabet must be mastered before it is possible to read. Had he become sufficiently mathematical to be modern —since modern genetics is so largely an exercise in applied mathematics—those for whom he wrote would certainly have failed to understand. Perhaps Hagedoorn felt, as Saint Paul felt, that:

". . . except ye utter by the tongue words easy to be understood, how shall it be known what is spoken?"

That his Gospel, although simple, *was* understood is proved by his popularity as a lecturer, his success as a consultant, his triumphal Australian tour when he was hailed by breeders as a scientific Messiah and, not least, by the wide and continuing success of his "Animal Breeding". Certain other criticisms of the geneticists I have attempted to answer in my addenda to the individual chapters of this book.

Somewhat curiously, Hagedoorn apparently rather despised the middle-man in science. ". . . I have a great distrust of the middlemen in science," he wrote—words that might seem in the nature of self-criticism because, in my view, it was in the rôle of just such a middleman that he achieved his greatest success.

He had a sound training in formal genetics although latterly it may well be that the genetics he taught was more reminiscent of Bateson than of Sewall Wright.

He had a profound understanding of the problems and practice of the animal breeder. I doubt whether any scientifically trained person has ever had an understanding equally profound. His extensive travels; his insatiable curiosity and his intimate contacts as a consulting geneticist gave him an insight

and a sympathy somewhat lacking in the average geneticist. Hagedoorn really appreciated the business he was anxious to reform. Apart from the Norwegian, Christian Wriedt, there have not been many other geneticists who have done so.

The business of the breeding of "pure-bred", "pedigree" farm livestock is one full of tricks. Hagedoorn knew them all. Yet even though the business be a tricky one and one in which obvious vested interest too frequently dons the mantle of an assumed and impersonal concern for livestock improvement, Hagedoorn never became accusative or didactic in his critical approach. He took the view—which is the only sensible view—that the pedigreed breeder is a man who, like most other men, is in search of a living and is no more likely to welcome devaluation of his products than is anybody else with goods to sell. Like Hagedoorn, I feel that the value of pedigreed livestock to animal production has been somewhat overrated; that some of the adulation of the successful breeder of such livestock is a trifle misplaced, and that a more objective, quantitative and realistic approach to the whole business of livestock improvement is long overdue.

The newer techniques of controlled progeny testing, sire performanee testing and so on are deserving of every encouragement but, if they are to be a genuine improvement on older methods, they require to be much more critically examined and rigidly controlled than is often the case. Figures for figures' sake could quite easily become as misleading and meaningless as pedigree for pedigree sake, and—to put the matter bluntly—to an astute business man it is probably easier to arrange figures for advertisement than to fit an animal for sale. Nobody realized this danger more clearly than Hagedoorn himself, and if, as seems probable, the sale value of quantitative records of production in farm animals tends to increase, so also will that danger.

There is no doubt that, whatever its alleged imperfections, this book of Hagedoorn's has done an immense amount of good. It has been very widely read both by students in agriculture and by practical breeders. At the very lowest valuation it must be admitted that, so far as genetics is concerned, Hagedoorn has played the rôle of a genetical Baptist, making smooth the way of those that come after.

Moreover, to anyone even mildly interested in Animal

Breeding, his is a most fascinating book. It contains so much diverse and unique information not to be found elsewhere: of how the Hopis and Zunis farm the Arizona desert; of how the successful exhibitor of Barnevelder poultry collected his birds for show; of how the stable-men in France practise the aphrodisiacal rite of "le lalandage" to induce the jack-ass to mate with his mares. It is a book full of personal experience, of anecdote, of human understanding and of profound common sense. It reads easily, like a novel, and is one in which, every now and again, between the more formal presentation of genetical theory, the vitality, wisdom and humour of its author come bubbling through.

Chapter Two

The Rôle of the Geneticist in Animal Breeding

The breeding of animals is based upon the fact that certain qualities of our domestic animals run in families. Breeders aim to work in such a way that the coming generations of animals will be as good as, or better than, the preceding generations.

The continued presence of valuable qualities in strains of animals is due to the presence of inherited developmental factors, which are passed on from parents to offspring. As the study of the transmittance of these substances is one of the main problems on which the geneticists are working, it is clear that this special knowledge of the geneticists may be of some value to the animal breeders.

When we want to co-operate with the breeders of plants and animals, we geneticists have to remember just where our interest coincides with that of the breeders, and we must be clear as to the breeders' objective, and how we can help them to reach it.

The aim of the animal breeders is to breed good, valuable or beautiful animals, and they must do this by manipulating the units in heredity, the genes. The breeders, however, are not interested in those genes as such. Years ago, when "Genetics" was a young science, some of us thought that the interests of breeders and geneticists largely coincided, that the co-operation between breeders and geneticists should be of great profit to both groups of workers.

It is true that to a geneticist, interested in evolution problems, a thorough working knowledge of evolution in domestic animals, in which changes are rapid, is very illuminating, and there may be one or two other points where a geneticist can learn by studying the work of the breeders. Where geneticists

co-operate with breeders, the breeders profit most, or should do this, if the geneticist knows his and their business.

The records kept by breeders, even the herd-book records, are seldom complete enough to permit a genetical analysis. This should never be a matter of reproach, because the records were not meant to be of interest to geneticists. I remember that at one of the international cattle-breeding congresses a committee of three men was nominated to study the way herd-books should be reorganized to make them valuable to genetics. This is really absurd. Herd-books need reorganization, but only to make them valuable to agriculture, and it is the task of geneticists to help to make them so.

To a certain extent making the herd-books and their registration methods better in regard to animal breeding would also make them more interesting as a source of genetic investigations, for the greatest weakness in the ordinary methods of animal registration lies in the circumstance that too many facts of great value are lost. A geneticist, turning to the register of a herd-book for a black breed of cattle would not find data on the inheritance of the one gene differentiating black animals from red ones, simply because the birth of red calves is not registered. From the standpoint of the pedigree breeders this seems good business, as it would hurt sales if it were known that some animals are heterozygous and apt to produce red calves. From the standpoint of the same breeders, however, the only way to get rid of the unwanted colour is to weed out the heterozygous animals, or at the very least the heterozygous sires.

In the interests of agriculture, it is important that the domestic animals fit into their place as perfectly as possible. For this reason the separate strains must be made pure-breeding, homozygous for the most perfect set of inherited factors, and the only way to do this is to gather complete data about the breeding performance of the animals used for reproduction. This means very complete registration and no hiding of defects. It must be recognized that the ordinary herd-books are not established to improve the breed; they register not from the standpoint of the users, but from that of the seller of breeding stock. The farmers who use the animals are not very likely to notice this, the pedigree breeders are prejudiced, and it is the task of the geneticists, who have no personal interest at stake, to point out such things.

I have considerable personal experience in co-operation with

practical breeders of plants and animals, and the more I engage in this, the more I am convinced that in helping the breeders we should not try to teach them much genetics. It is absolutely necessary that the geneticist himself shall have a clear picture of the why and wherefore of different systems of selection, and it often helps to be able to explain these things to an intelligent breeder. The geneticist, however, should not try to analyse the differences in the genotype of the animals up to a point where all the different genes concerned can be labelled and lettered. He should clearly understand that gene-analysis is an important tool in experimental genetics, necessary to obtain an insight into the working of the genes and their co-operation with environmental factors, but that the only genes we can hope to analyse are those that happen to have a very striking influence upon the development in the conditions of the experiment. In genetical experiments we carefully choose our genes and their substratum to get a clear picture, but when we are concerned with differences in quality between domestic animals, we must work with the genes influencing the qualities, whether we can recognize them as separate or separable factors or not. An animal breeder has to manipulate genes and genetic differences due to very many genes, and the important thing is that he shall choose the correct method of doing the work, whether he ever knows those genes as such or not.

The geneticist's main contribution to animal breeding is not an analysis of genes, but an analysis of breeding methods. Starting from the assumption that the material comprises many individuals heterozygous for numerous genes, he must show the way in choosing methods of working, which must result in purity for the most favourable combination of genes.

To get together with the breeders he wants to co-operate with, the geneticist must meet them half-way. He must learn to speak their language, he must understand their terms, and above all things he must understand their aims and their difficulties. Preaching is the worst thing he can do. When, as often happens, breeders of certain groups of animals use absolutely wrong standards of value in their breeding aims, it does no good just to tell those men that they should choose their best breeding stock in some wholly different and more logical way. First, he must try to discover for himself why those breeders should set themselves such false goals, but in the meantime he must learn

to see eye to eye with the men he thinks are mistaken. Very early in my career as a consulting geneticist I learned that it is absurd for a geneticist to ask a farmer to accept his own revolutionary views, when he cannot win the respect of the farmer by being able to tell the good and bad points of a cow or a horse. After all, it is far from difficult to learn what a showman admires in the shoulder of a horse or in the tail of a cow, and if knowing those things will bring about a better understanding between the man of science and the practical man, it is foolish not to avail oneself of this occasion to make those mutually valuable contacts.

In some ways a practical breeder has more experience than a geneticist in regard to the particular animals the breeder is interested in. On the whole the main advantage a geneticist has in helping the breeders lies in the fact that his experience in matters pertaining to selection is vastly superior to the experience the breeders can have. In the first place, the experience of an old hand in this sort of work is the sum of the experience of the breeders with whom he has co-operated. In the second place, the principles of heredity being identical in all living beings, the geneticist works at a much wider and higher plane than each particular breeder of one sort of livestock. Very often seemingly insoluble problems that confront the breeders of one particular kind of animals are not really problems at all: they have been solved over and over again in very similar instances in other animals, and often in plants.

Nobody has ever bred in-breeding-resistant strains of poultry and poultry breeders often discuss the question whether it will ever be possible by continued in-breeding of brothers to sisters to obtain a strain that will be wholly pure and in which no further selection will be necessary or even effective. To geneticists this problem is not a problem at all. We know from experiments with other animals and with plants that it will be possible to do this, and we are also able to point out the abundant snags that will present themselves to breeders who want to do this work.

When Mr. H. W. Kuhn, the sugar-beet authority, became a member of the Herd-book Society he later presided over for so many years, and gave his opinion on a question of selection in cattle, somebody questioned his experience, as he was only a cattle breeder in a very small way; but he could truthfully say

that, in matters of selection, his experience was a hundredfold that of his most experienced colleagues who were cattle breeders, because he had been selecting sugar-beets all his life.

A geneticist co-operating with breeders should follow the actual breeding work of different men very closely from year to year. Perhaps the very best thing he can do to obtain experience is to do some animal breeding himself. I think that, for my own part, the making of a few new breeds of poultry, and breeding some different kinds of fur animals, in addition to the more extensive breeding operations with small animals with the object of solving problems of theoretical interest, has done much more to give me an insight into the practical problems of my friends the animal breeders than anything else.

A young geneticist, starting to co-operate in animal breeding, is soon brought to the point where he must choose between working with the breeders themselves or with the animal-breeding authorities. It is a very curious thing that almost in every country in which I have lived for some years a sort of antagonism exists between the breeders and the authorities directing matters of animal breeding. The same thing was true in plant-breeding when the reorganization of plant-breeding methods under the influence of genetics was at its height.

I generally find that the practical men who do the work and who are in close personal touch with all the practical details are very much less likely to be deceived by plausible-appearing, but unfounded theories than the authorities. The fault, I believe, lies in the fact that the men in authority, such as farm advisers, instructors in animal breeding, etc., usually lack the background experimentation ought to give them. In the chapter on Government influence I have gone more deeply into this question.

It is my oft-repeated experience that the practical men are generally much more progressive and open to new truths than those set in authority over them. Some of the most antiquated notions, which have been disproved time after time, still exist in the minds of some of the older men. It is hopeless to try to convince such men. I am fully in accord with Boutflour that such men are incapable of learning: they must die out and be replaced by younger men who have learned more than their predecessors.

I have often found that it was necessary to go over the heads

of the learned men in authority to reach the practical men who are eager to profit by the lessons geneticists can teach them.

In plant breeding a similar state of things existed when plant breeding was about as backward as animal breeding is to-day, about forty years ago. At that time the "higher", scientific plant breeding mainly consisted of attempts to find characters correlated with yield and other economically-important qualities, but at the same time the practical plant breeders in their small institutes and in the seed-firms were already forgetting all this solemn tomfoolery, and, with the aid of geneticists like Biffen, Nilsson Ehle, Baur and others, were learning to use the relatively simple, empirical, foolproof methods of to-day.

In animal breeding things are tending in the same direction. Thirty years from to-day breeders will hardly be able to believe, that even as late as 1930 or thereabouts people were so foolish as to think that selection for show points in cattle was helping to build up the correct sort of constitution, or that licensing of stud stallions was still done without any relation to progeny testing, or that there were countries in Western Europe where a system of selecting poultry based upon the production of individual hens was forced upon the breeders by the Government.

Most geneticists who interest themselves in applied genetics are botanists taking up plant breeding. Very few of my colleagues interest themselves in animal breeding. Outside of America there are perhaps twelve of us, all told. Notwithstanding this, or perhaps I ought to say for this very reason, animal breeding and co-operation with animal breeders is a fascinating field of study for a geneticist with the necessary "fighting spirit".

I am greatly in favour of a direct co-operation between real geneticists, with an experimental background, helping to build up the science, and real animal breeders, and I have a great distrust of the middlemen in science. Once in a while blatant stupidities are foisted upon the unsuspecting laymen in the name of our science. In the chapter on progeny-testing I have treated of one of those monstrosities, the "genetical analysis" of fat content in milk by means of four utterly improbable "genes".

Personally I have always obtained very much satisfaction from what I have been able to do in co-operation with the animal breeders. One man working alone can only touch upon

the most important subjects here and there and point the way for the younger colleagues to go. Animal breeding, perhaps more than plant breeding, needs the foundation of special institutes of applied genetics, where the many problems touched upon in this book can be fully worked out in the interests of agriculture.

NOTES

"I have a great distrust of the middlemen in science."

This statement of Hagedoorn's, at first sight, might seem to be an unusually forthright expression of frank self-criticism since it is precisely in that capacity—as a "middleman" between the scientific geneticist and the practical breeder of farm animals—that Hagedoorn and his book on "Animal Breeding" have had their greatest significance.

Yet I do not think that Hagedoorn had the slightest intention of being self-critical, since one of the many reasons for the success both of the man and of his book lies in their breezy self-confidence. The point, as I see it, is that Hagedoorn, far from regarding himself as a middleman, considered himself to be a geneticist first and foremost, and his function to be the carrying of the torch of genetics into the shadowy recesses of animal breeding, his mission that of a Messiah rather than of a middleman. It is, therefore, perhaps somewhat ironical that geneticists themselves have never been particularly impressed with Hagedoorn's genetics!

A common criticism voiced by his fellow geneticists is that Hagedoorn's genetics are out-dated in that he seldom pushed his analysis beyond the simple, easily understood and somewhat rare monofactorial Mendelian ratios and that he deals in an entirely qualitative manner with a subject which, in more recent times, has become highly mathematical.

To me, it seems a sufficient answer to such criticisms to emphasize in Hagedoorn's own words that his book on "Animal Breeding" was "a book destined for the breeders themselves". Now, a book, to be useful, must be read, and had Hagedoorn written a different type of book such, for example, as Lush's "Animal Breeding Plans", very few breeders indeed would have read it. By adopting a different and simpler approach Hagedoorn secured a large and enthusiastic audience among the precise public he aimed to influence.

Whatever may be said or written of Hagedoorn as a geneticist, the most critical of his fellow geneticists is bound to admit that Hagedoorn, more than anybody else, prepared the soil on which other geneticists, should they wish to do so, may now sow. In doing this, he very manfully, just like Boutflour, was prepared to wield the sickle of science to clear the practice of animal breeding from a jungle of weeds.

It is no easy task to preserve the smile on the face of a man going to the guillotine, yet that, precisely, is what Hagedoorn succeeded in doing. He

gained the confidence of practical breeders while he was, at the same time, hewing down their sacred groves of custom and superstition, laying low the battlements of their vested interests embodied in their Breed Societies with Mosaic ruthlessness and determination. How he succeeded in doing so is enshrined in certain passages of this chapter, passages which many of our younger geneticists concerned in animal breeding would do very well to ponder.

"To get together with the breeders he wants to co-operate with, the geneticist must meet them half-way. He must learn to speak their language, he must understand their terms, and above all he must understand their aims and their difficulties. Preaching is the worst thing he can do. When, as often happens, breeders of certain groups of animals use absolutely wrong standards of value in their breeding aims, it does no good just to tell those men that they should choose their best breeding stock in some wholly different and more logical way. First, he must try to discover for himself why those breeders should set themselves such false goals, but in the meantime he must learn to see eye to eye with the men he thinks are mistaken."

It is still a common fallacy to regard farmers of all types, animal breeders included, as ultra-conservative and rustic Hodges, stuck fast in the mud they work in. That is not my personal experience, nor my personal view. Rather, as with Hagedoorn, it has been:

". . . my oft-repeated experience that the practical men are generally much more progressive and open to new truths than those set in authority over them."

That is plain statement of fact. An unsuccessful farmer will end in the Bankruptcy Courts. An agricultural scientist, equally unsuccessful, may find refuge on an Advisory Committee.

In his respect for and courtesy towards "the man on the job" Hagedoorn emphasized the essential preliminary for any geneticist attempting to play a useful rôle in the industry of animal breeding.

Chapter Three

Animal Breeding compared with Plant Breeding

The laws of heredity that govern reproduction are identical in all living organisms—in plants, in animals and in man. For this reason it would seem that there would also be an essential similarity between the principles of animal breeding and of plant breeding. In fact, however, plant breeding and animal breeding differ in a surprisingly large number of points.

When, in the beginning of the twentieth century, the re-discovery of Mendel's principles furnished the key that made it possible to discover the real nature of heredity, the plant breeders were very quick to see the possibility of applying these discoveries to improve their methods of plant improvement. During the first ten years of the century we witnessed a veritable revolution in plant-breeding technique; and it can be said that there are very few plant-breeding methods left which could be improved upon by a critical geneticist. Plant-breeding methods are genetically sound.

In animal breeding we are a long way from this ideal condition. Speaking in a general way, the methods of animal breeding, especially when contrasted with those of plant breeding, are remarkably speculative and economically wasteful. We can point to a few exceptions: there are some poultry breeders who have reorganized their methods and who have obtained gratifying results, but even in the breeding of poultry the majority of breeders still muddle along with genetically unsound methods of selection which make them lose an unnecessarily large amount of money every season.

Why is it that in sound business methods animal breeding

lags so far behind plant breeding? Several different causes contribute to this. The first of these lies in the circumstance that, from an economic standpoint, the production of agricultural crops and agricultural animals is very much more important than the breeding of any other category of plants and animals; and especially in the agricultural plants and animals there is an enormous difference in the relative value of one individual as compared with the breed.

In wheat, in sugar-beet, in flax, the quality of the breed as a whole, the value of a large field of plants is important, but each individual plant is relatively valueless. For this reason plant breeders are more likely to attach importance to the average quality of large plots of plants than to the individual quality of separate plants.

In horses and cattle, an important amount of money is invested in every individual stallion, every individual cow. Each owner only owns a comparatively restricted number of animals; he knows them all as separate personalities, and hence the individual in his mind is of very much more importance than the breed to which it belongs.

For this reason a plant breeder is more likely than an animal breeder to think in terms of groups of individuals rather than in terms of individuals, and in selection and breeding practice this is extremely important.

The second point of difference lies in the rapid reproduction of plants as compared with animals. Whereas in the larger farm animals it takes approximately two or three years to produce another generation, and five or six years for a group of animals to double in number, in agricultural plants we have a generation every year, and every year we can multiply the number of individuals a thousandfold.

The main result of this difference is that in agricultural plants it is feasible to separate the multiplication of a breed from its economic use, whereas this is practically impossible in most of the agricultural animals. In ordinary farm routine, the farmer buys his seed from a specialist, but he breeds his own cows and horses. The production of sugar-beet seed, the production of seed wheat, or of onion seed, is in the hands of a few specialists who do nothing but multiply and select these agricultural plants. The breeding mares and cows, however, are in the hands of hundreds of thousands of people for whom

the daily use of these animals comes first, whereas breeding almost always comes in a secondary place.

One of the consequences of this concentration of the breeding of agricultural plants in specialist firms and in Governmental and similar breeding-experiment stations has been that trained geneticists have in these institutions devoted their lives to the genetical aspect of this work of selecting and improving of agricultural crops. The decentralization in animal breeding, however, has withdrawn animal breeding from the sphere of influence of the geneticists.

A centralization of animal breeding has not been wholly lacking, for breeders of several breeds of agriculturally important animals have formed associations, breed societies, herd-books: but in the very nature of these associations there enters a very curious element. The breeders who come together to form these herd-books are not necessarily the general run of farmers, who are the real users of the animals and who would be primarily interested in improving them from an economic standpoint. They form a special group of breeders who are primarily interested in selling breeding stock, and for this reason more interest exists in the selling points of the breed and of outstanding individuals in the breed than in points of real economic value when the two do not happen to coincide.

In some instances the standards of excellence used by the herd-books in the real or fancied interest of the members have no relation to real economic value, and where this is realized, a difference of opinion often exists between the users of the animals and the geneticists on one side, striving to set up real economic usefulness as a standard of merit, and the herd-book on the other side, striving to keep going the old system, which makes it possible for the members to sell a good number of young untried bulls and of young stallions with good looks but otherwise only of speculative value.

There is one other difference between plant breeding and animal breeding when looked upon from a genetical standpoint. We geneticists have often stated that the ideal way in which a practical breeder and a geneticist must co-operate is a system in which the practical man tells his aims and his troubles to the geneticist and the latter helps him to overcome those troubles and to attain those aims. In plant breeding this works very well indeed. We must realize, however, that this is mainly

so because the aims of the plant breeder are relatively simple and straightforward—aims that can be easily grasped and understood. With most plants the ideal is to produce the greatest amount of crop of high quality per unit of area.

In animal breeding, however, the aims of the breeders are not so simple or so straightforward. In not a few instances the aims of the breeders have not been well thought out. It is astonishing to observe how often even the breeders of economically-important breeds of animals, such as milk cattle, set up a standard of excellence that comprises a good number of wholly irrelevant fancy points—such as colour, length of the dorsal excrescences of the vertebrae, resulting in a special back-line, shape of the horns and such things. Even when the aim is production, the way of judging merit may be such that real economic value is lost sight of in favour of some single one of the characters contributing to the economically-excellent result. When, e.g., breeders of milk cattle look for pounds of butter from a cow, or when breeders of hens look for number and size of eggs alone, and lose sight of food-consumption or other factors in the economy of the animal, I am always reminded of the fat man in Wells's story who took a magic remedy to "lose weight"—and had to live floating against the ceiling of his bedroom!

The real truth of the matter seems to be that whereas geneticists can help the plant breeders to attain their aims, somebody has to help the animal breeders to set up economically useful aims before they can be helped to attain them.

Some geneticists have seen that a whole lot of preliminary work of this kind must be done before we can hope for animal breeding to be put on a footing similar to that of plant breeding. Cases in point are the reorganization of laying tests for poultry and statistical investigations on methods of selection in cattle.

Whereas in plant breeding the pioneering work of reorganization of breeding methods was practically all done by 1910, animal breeding, with a few outstanding exceptions, has stood still up to 1930, and just now we can only say that in animal breeding the influence of a better insight in variation and heredity is beginning to cause similar changes in method to those in plant breeding forty years ago.

The outstanding exception to the rule that almost every-

where animal breeding has stood still while plant breeding has progressed has been Denmark. While my colleagues and I in England and Holland tried in vain to get the animal-breeding societies interested in rational methods of selection, the Danish co-operative farmers' unions were going ahead practically alone. One of the chief reasons why rational animal-breeding methods could be used in Denmark is the circumstance that in that country the change from general mixed farming to grazing was accomplished comparatively recently. In Denmark, modern methods of animal breeding did not have to struggle against an old-established tradition of doing things in a certain established way.

In the breeding of certain kinds of animals, the difference between agricultural animals and agricultural plants is not as marked as in breeding cattle and horses. The more fertile an animal is, and the less value every individual animal has, the more likely is it that rational methods of selection according to genotype will be substituted for the old-fashioned way of selecting according to individual merit.

In plant breeding the greatest successes have been attained by substituting a system of selection, in which breeding value is the real test of superiority, for a system in which every individual plant is judged according to its own merits. The reason for this lies in the circumstance that a favourable set of non-hereditary developmental factors, such as a favourable spot, specially advantageous conditions of climate and lack of competition, may have such a great influence upon the qualities of that particular plant, that those qualities do not constitute a good criterion by which to judge the plant's heredity. If we judge a larger group of plants, all descended from one common ancestor, the variations in the circumstances under which the plants in this group grew up tend to neutralize each other's action, so that the quality of the group of descendants gives us a better way to judge of the heredity of this common ancestor.

In breeding animals, it seems so obvious that the only certain way to judge an individual as a breeder is to judge the quality of his descendants that it seems absurd that geneticists have had to work hard to make the animal breeders accept this simple truth. Several different things have contributed to this difficulty. To defer the judging of a stud horse until we can actually do it by noting the quality of his get seems a very

slow way of doing things, when we are convinced that there are simpler, quicker methods. In many instances, as in the first choice between a great number of young males, the majority of which are superfluous, a choice has to be made at an early age. It is perfectly obvious that the farmer who must kill off at least eighty per cent. of his bull calves chooses for survival those that best conform to his ideal of beauty: and it is obvious that ideals of beauty, such as can be judged so easily at an early age, tend to become more popular than their value merits.

Most animal breeders are so used to a great variability in their young animals, and the necessity of culling a great many, that they tend to forget the culls and to judge an animal's breeding value by the quality of his very best descendants. This is unsatisfactory.

Whereas plant breeders are continually comparing the merits of different breeds, ready to discard one breed when they find a second one is better, most animal breeders are convinced that they will be able to change the quality of the one breed to which they are accustomed.

In reality animal breeders tend to overrate the genetic variability within the breeds, so that often they are attempting the impossible. Very often new breeds tend to displace old ones, but only rarely this is a matter of deliberate choice as the outcome of suitable comparisons and experiments.

In many aspects animal breeding could profit by the lessons to be learned from plant-breeding practice. In different ways and at different times it will be necessary to use plant-breeding methods to illustrate points, and it will be possible to hold up plant-breeding methods as an example to animal breeding.

Maize-breeding Methods compared with Animal-breeding Methods. The experiments of George Shull and those of East and Jones with maize in the U.S.A. have finally led to commercial methods of seed-corn production that are based upon the superiority of hybrids. Sometimes two varieties are chosen, it being known that the hybrids are of superior quality. The plants of one variety are detasselled and in between several rows of these, plants of the variety used as the father furnish the pollen to secure the hybrids. Such hybrid maize often produces a yield of grain that is very much higher than that of the in-bred lines crossed.

This high yield of the hybrid plants, compared with that of the separate in-bred lines crossed, is due to the combination of genes derived from both parents, and so long as this combination of the two breeds furnishes the right combination of genes in all the hybrids, it does not matter much whether the in-bred lines themselves are very poor yielders.

This, however, is not absolutely true. Sometimes those in-bred pure lines have so much gone down in yield that the mother plants are poor yielders, and that the cost of hybrid seed becomes too high. There are two ways of overcoming this difficulty, and the most obvious one is to produce a triple or even a quadruple cross, namely to use hybrid plants as mothers and a pure in-bred strain or even another first generation cross as the father of the seed sold. This is the usual method, thoroughly advertised. Another way is the use of non-in-bred highly productive plants as mothers, top-crossing them with in-bred fathers of another strain or breed.

We must remember that the very high production of the hybrid plants is considerably flattered if we compare it with the miserable yield of one of the highly in-bred lines. To judge whether the in-breeding really gives us better material for the cross we should compare the quality of hybrids between in-bred lines with hybrids between non-in-bred pure breeds. If we do, either in maize or in sugar beets, it is found that the value of the in-breeding work is highly overrated.

When it is proposed to apply a similar method to poultry, pigs or milk-cattle in addition to sheep, for which the method is employed, we must carefully determine what its advantages and disadvantages are.

In maize breeding the advantage of a single cross over a triple cross, involving three lines, lies in the greater uniformity of the resulting crop. If our best in-bred line only gives us a few miserable heads, the commercial seed produced is expensive and looks very poor. For this reason cross-bred plants are generally used to furnish the seed, when pollinated with another, third, variety, notwithstanding the circumstance that a much more variable harvest results. Even with maize a much better scheme would be to use a fully viable and productive line to furnish the seed, and to use a suitable in-bred second line for the pollen parents.

In poultry, and especially in our larger animals, the fertility

is so low when compared with sugar beets or maize, that such cross-breeding schemes can only pay when the breed that furnishes the females will pay its way by itself. In the poultry schemes that depend upon cross-breeding, nobody could make these work when the breed that furnishes the eggs did not produce a good many at the right season.

Plain in-breeding without selection in any breed that is full of impurities will in most instances result in stock that happens to be pure despite many bad faults. The object of such complicated breeding schemes, where in-bred strains are produced, to be crossed later, can only be to produce the required degree of homozygosity. We must remember that when we start in-breeding with any group, those animals are already homozygous in respect to a great many genes, while heterozygous for others. In-breeding makes the group homozygous for those genes in respect to which heterozygosity still existed. If a number of individuals are heterozygous in respect to *B*, ultimately the group when in-bred will consist of all *BB* or all *bb* individuals.

If we suppose factor *B* to be valuable, the loss of *B* in a *bb* group can never be an advantage. For this reason we must not leave the genotype of an in-bred group to chance. Selection will be necessary to make the in-bred lines better fitted to give valuable first-generation offspring. The advantage of a cross-bred group over variable pure-bred groups can only lie in the combination of valuable co-operating genes in the hybrid lot. It is much more important to find the correct combination of breeds to cross than to obtain a high degree of purity in both those breeds. If the best combination is not found, an improvement of the strains by selection will not help very much.

I venture to think that the importance of in-breeding in the breeds to be crossed is overrated. The striking improvement of constitution and yield in the hybrid group is due to some extent to the contrast between the greatly diminished quality of the in-bred groups and the hybrids.

Insofar as a group of hybrids is better in health, in resistance to disease and in yield when compared with one of the strains or species crossed, the possibility certainly exists of ameliorating that breed by means of cross-breeding. If the hybrid is superior because in addition to the genes of one of the parental groups it possesses one or two additional genes derived from the other

variety, back-crossing the hybrids with this parent group will make it possible to add this quality. In fact, there is no clear demarcation line between this and what is discussed in the chapter on adding a gene (Chapter Sixteen).

NOTES

In this chapter, Hagedoorn draws a comparison between Plant Breeding, which he evidently considered to be based on sound scientific principles of modern genetics, and animal breeding, which he considered to be very much the reverse.

It seems to me that here there are two separate questions to be discussed. In the first place, while in Plant Breeding there is a clear division between the man or organization growing the seed and the farmer who buys it to sow his crops, that division of labour is, admittedly, less clear in Animal Breeding. With the passage of years and the development of A.I., however, it is becoming more marked. I don't think it was ever quite so indistinct as Hagedoorn suggested when he wrote that:

"The breeding mares and cows, however, are in the hands of hundreds of thousands of people for whom the daily use of these animals comes first, whereas breeding almost always comes in a secondary place."

Is this statement really true? Surely not so far as the stud-breeder is concerned! While very frequently there may well be a combination of enterprises there is still in cattle, sheep, pigs, indeed in all livestock production, the man who specializes in producing breeding animals to sell, be it a pedigreed, pure-bred bull, ram, or boar, and the man who buys these sires to use in the production of milk or beef, mutton or wool, beef or pork. Now, on Hagedoorn's reasoning, a further and firmer separation and greater distinction between the "stud-breeder" and the "commercial" livestock producer would be an advantage, since it would bring Animal Breeding into closer alignment with Plant Breeding.

I am somewhat doubtful of that proposition unless, indeed, the stud-breeder were prepared to progeny test his stock under the "commercial" conditions in which the business of his customers are conducted. I have felt sometimes that the separation of aims and interests between the stud-breeder who sells breeding stock and the "commercial" farmer who must use them is one of the very weakest links in present-day systems of animal husbandry.

In the second place, I very much doubt, also, whether plant breeding, as contrasted with animal breeding, is invariably conducted on strictly genetical principles, without regard to other considerations not strictly genetical. After all, seed production is a trade, and there is no trade without tricks. I make no pretensions whatever to any specialized knowledge of plant breeding. I have, however, in the more humble capacity of a household gardener, bought new

"varieties" of flowers which have very quickly reverted to something much less novel in a cottage environment. The late William Findlay, with his vast experience of cereal crops, of clovers, and of grass, told me of his rather similar experience in a wider field.

Hagedoorn, at one time a geneticist employed by a seed firm, suggests in this chapter that in modern seed production the principles of Mendelian genetics, fully understood and intelligently applied, is the secret of successful progress. He was in a position to know and I have not the first-hand knowledge to dispute his claim. Others possessing such knowledge might, however, be prepared to contest it, as for example Hudson and Richens did when, in reviewing "The New Genetics in the Soviet Union", they wrote that:

". . . many plant breeders would admit that genetical theory has had little or no direct influence on their practical methods, and has contributed relatively little to their achievements."

Chapter Four

Heredity

The animals of one species, of one breed, resemble each other, and this resemblance is due to heredity. If we mate Guernsey cattle we expect a Guernsey calf, and if we breed White Leghorn fowls we expect the chicks to be White Leghorns.

When the new science of Genetics was in its infancy, it was generally believed that the process of inheritance consisted of the transmittance of the qualities of an individual to its offspring. To-day we know the mechanisms of the process which is responsible for the similarity between parents and offspring, and as a result we now know that it is scientifically inadmissible to say that certain qualities are inherited from parent to offspring. The old controversy about the question whether acquired characters were inherited was based upon a misconception of the nature of inheritance, as we shall presently discuss.

When we look at an adult animal and compare it with the germ-cell from which it grew up, we find that the qualities of the adult animal are acquired in the course of a process of growth of development. To a certain extent, the final result of the development is due to qualities inherent in the germ-cell in the fertilized ovum, but at the same time we know that this germ-cell can only grow and develop when external conditions are just right.

The final qualities of an animal are due to the way it develops, and this development is the result of the co-operation of a great many different things, which we may call factors in this development. Those developmental factors are always of two fundamentally different kinds, inherited factors and non-inherited, environmental factors.

Notwithstanding the fact that the nature of the two kinds of factors in an animal's development is wholly different, it is not possible, in a general way, to say that the inherited factors are more important than the environment; or the other way round, at no time is it possible for a young animal to keep on developing, when both kinds of factors do not co-operate to this development.

The inherited developmental factors are of one very special kind: they are material substances that are passed on from parent to offspring. When the egg produced by the mother is fertilized by one sperm, furnished by the father, the egg and the sperm contain a great many of those substances. The fertilized germ contains an enormous number of these substances, and very little of each. These inherited substances are derived only from the parents, and once the egg is fertilized, the set of inherited substances this egg and the animal that grows from it will ever have is determined once and for all.

In Genetics we call those inherited substances, which are factors in the development of an animal, by the name "genes": and we employ the term "genotype" for the make-up of the individual, as far as those genes are concerned.

The genotype of an animal, therefore, is made up of a great number of genes, and the genotype of that animal is unalterable. To a certain extent the animal's inherited make-up makes it possible to develop in certain ways, and the genotype also sets certain limits to this development—but the final qualities of an animal are not wholly determined by its genetical make-up, as in every quality non-genetical developmental factors have some influence.

When the fertilized ovum begins to develop, the first cell divides into two cells. These again divide, and the four cells so formed divide again and again, until finally the large, complicated animal, consisting of millions of cells, has grown from the microscopically small germ.

Those cells of the adult organism differ from each other in several ways—in size, in shape, in chemical and physical properties: but still we know that in one respect all the cells of the animal are alike, for they all contain the original set of genes which went into the fertilized egg.

It would be hard to understand how it could be possible for all the cells to contain the same substances, when we know dif-

ferent kinds of cells differ so much in composition, if we did not know that the genes within the cells are localized in a separate nucleus. Inside this nucleus the genes are arranged in strings, the chromosomes; outside the nucleus in the cell cytoplasm other cell-ingredients are present in varying proportions in different tissues.

The chromosomes in the nucleus are paired, and in every pair one chromosome is originally derived from the mother and one from the father. When a certain gene is inherited from both parents, the chromosomes are so arranged in the nucleus that those two genes are placed side by side, and this is possible for all the genes, because they are arranged in a definite order on the chromosomes.

In the higher organisms every cell contains a great many genes, and it is evident that the number of different genes runs into the tens of thousands. In the beginning it was thought that those genes would probably be protoplasmatic, living corpuscles, but it becomes more and more probable that we are dealing with chemical substances of a special kind (autocatalisers), and that only one molecule of each gene is present in each cell.

The genes multiply in the cell, and when every gene present has doubled its volume, the whole chromosome splits into two identical halves. Before every cell division the chromosome pairs go to opposite poles of the nucleus, which divides before the cell does, and in this way one complete cell containing a pair of chromosomes of each kind for a short while contains two pairs, and then divides into two equivalent cells, each having one pair of each chromosome.

In Genetics it has become usual to denote genes by means of letters of the alphabet. If both the father and the mother have contributed a certain gene *A* to the fertilized egg, the egg nucleus, as far as gene *A* is concerned, becomes *AA*. By duplication these two *A*'s become four, so that for a short while the nucleus contains *AAAA*. At the next nuclear division and cell division, we get again two complete cells, each containing *AA*.

Now any cell can only be in one of three possible conditions in respect to any given gene. The case in which both parents contributed *A*, we have just discussed. It is possible that the parents did not both contribute the same gene. If at the moment of fertilization, only the egg or only the sperm contains *A*, in the chromosomes at one spot there will be a gene *A* in one

of the pair, but the other chromosome of the pair lacks it. Usually we employ small letters as symbols for the absence of genes, and then the nucleus of the fertilized egg will not be *AA*, but it will be *Aa*. When now the nucleus starts to divide, there will be a moment when there are four homologous chromosomes in the nucleus, *AaAa*, but when the nuclear division is complete, we have two cells that both have the original *Aa* composition.

In such a case we say that the individual is "heterozygous" for gene *A*. In such a heterozygous individual, every single cell of the body is equally heterozygous, and carries *Aa* instead of *AA*.

The third possibility is that *A* is lacking from the original cell altogether, and we can then write its formula *aa*.

For a certain gene *A* there are therefore three possible conditions in which we can find individuals, namely, *AA* (homozygous), *Aa* (heterozygous), and *aa* (absence of the gene).

At the time of fertilization the nucleus of the germ-cell is composed of the chromosomes in the egg (derived from the mother) and the chromosomes in the sperm. Let us say that each parent contributes four chromosomes, so that the fertilized germ-cell contains four pairs. We saw that every cell of the young organism has the genotype of the original germ, in this case four pairs of chromosomes.

Eventually such an individual becomes sexually mature, and starts to produce germ-cells. It is evident that there would be a doubling of the chromosome number at every generation, if the germ-cells contained a full complement of chromosomes, just like all the body-cells. If every egg and every sperm contained four pairs of chromosomes, the new fertilized eggs would contain eight pairs, and if this process went on, the number of chromosomes would double in every generation.

This, however, does not take place, for every organism produces germ-cells in a special way, destined to halve the number of chromosomes present in the body-cells. Whereas in every ordinary cell division the nucleus divides after the chromosomes have duplicated, this so-called reduction-division consists of two subsequent divisions after one chromosome doubling.

When an animal in its germ, and as a result of this in all its body-cells, carries a pair of chromosomes in both of which *A* is present, its formula may be written *AA* or *AAAA* after the chromosomes have duplicated just before nuclear division. At the reduction-division four cells are formed, each containing

one of those chromosomes, and as a consequence each only containing one *A*.

When a homozygote produces germ-cells, "gametes", those germ-cells will all contain the gene for which the individual was homozygous.

What happens when a heterozygote produces germ-cells? In a heterozygote, only one chromosome of a certain pair carries *A*, the other does not. We can write the formula of its body-cells *Aa*. Just before each nuclear division a cell becomes *AaAa*, and when a reduction-division takes place, this gives us four gametes, *A*, *a*, *A*, and *a*. In other words, a heterozygote produces two kinds of germ-cells, 50 per cent. with and 50 per cent. without the gene, which was inherited from only one parent. It is evident that an animal that did not receive a certain gene from either parent will not be able to pass it on to its children, and the *aa* individual will produce nothing but *a* gametes.

In respect to one gene, *A*, we may have:

(1) Both germ-cells containing *A*, fertilized ovum *AA*, body-cells *AA*, own germ-cells all *A*.

(2) Both germ-cells lacking *A*, fertilized ovum *aa*, body-cells *aa*, own germ-cells all *a*.

(3) One germ-cell with, and one without *A*, fertilized ovum *Aa*, body-cells *Aa*, own germ-cells 50 per cent. *A*, 50 per cent. *a*.

In a few instances it is possible to demonstrate the presence of a gene in the germ-cells themselves. In ordinary rice exists a certain gene that is necessary for the production of starch. In "ketan", glutinous rice, this gene is lacking. When we cross the two kinds of rice, we make heterozygous plants, which in respect to this gene are *Aa*. Now if we treat pollen-cells (gametes) of rice with iodine, they become dark blue, but pollen-cells of ketan do not change colour; when we treat some pollen from the heterozygotes with iodine and examine it, we find a mixture of dark blue (*A*) and pale (*a*) gametes.

It is very rare to be able to demonstrate the presence of a gene in germ-cells directly. No instance is known in animals. We can, however, see the production of two kinds of germ-cells, 50 per cent. with and 50 per cent. without, in a heterozygote, when we are dealing with a gene, which influences development in some marked way.

In animals in general the presence of one dose of a gene, as in

Aa animals, causes as much change in development as the presence of two doses in *AA* animals.

In ducks there is a certain gene which (together with a lot of others) must be present in a duckling for it to develop pigment. Animals lacking this gene are white. If we mate a coloured drake with white ducks, we know that the resulting coloured ducklings are heterozygous: they can have inherited *A* only from the coloured parent, and for this reason they must be *Aa*.

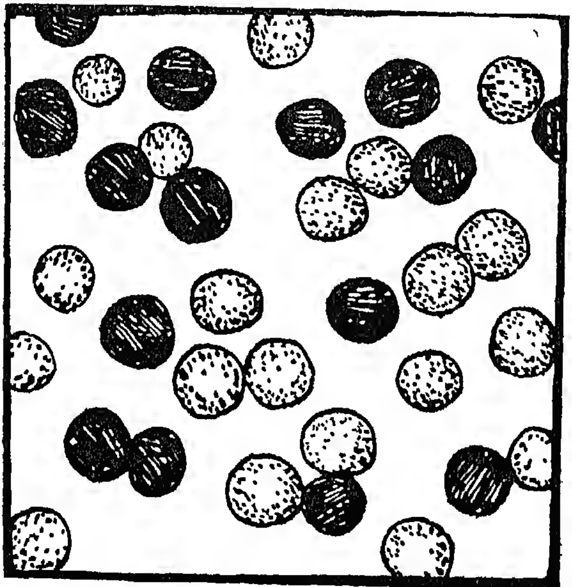


FIG. 1.—Pollen of a hybrid between ordinary rice and glutinous rice (ketan), after treatment with iodine (after Parnell). Rice pollen stains an intense blue, ketan pollen becomes yellowish; the hybrid pollen is of two kinds.

To find out what kind of germ-cells such animals produce, the easiest way is to mate them back to whites, for we know that the whites lack *A*, and all their germ-cells must be *a*. When we do this, we get 50 per cent. coloured and 50 per cent. white ducklings. The coloured ones must have inherited the factor *A* from the coloured, heterozygous, *Aa* parent and the white ones came from two *a* gametes.

An individual that proved to be homozygous for a gene *AA* will always give factor *A* to all his offspring. Such a homozygote originates from the combination of two gametes, both carrying gene *A*. It is clear that the parents of a homozygote need not be

homozygotes: for if we mate two *Aa* animals together, both of them will produce 50 per cent. *A* gametes, so that they will produce some homozygotes, *AA*.

This mating will also produce some more heterozygotes, *Aa*. A heterozygote is simply an animal which is born from two gametes, of which only one contains the gene, and it is not necessary that the parents of a heterozygote produce nothing but just one sort of germ-cells. The coloured ducks born from one coloured and one white parent are surely all heterozygous *Aa*, but other heterozygotes will be produced from all matings in which it is possible for an *A* gamete to unite with an *a* one.

On Dominance. We have a case of complete dominance if two doses of a gene in a homozygote have the same effect as one dose in a heterozygote.

Sometimes, however, it happens that the heterozygotes (*Aa*) are more or less intermediate in character between the two homozygotes, *AA* and *aa*. A very good example is that of the three colours in Shorthorn cattle. Here the roans are heterozygotic (*Aa*) and the red or the white animals are *AA* and *aa* respectively.

Whether dominance is or is not complete depends upon the rest of the hereditary make-up. Barring in chickens, for instance, is dominant in black-downed breeds, so that there is no significant difference in colour between *BB* and *Bb* chicks. In brown-downed breeds, however, the *BB* birds are very much paler in colour than the *Bb* ones, and the existence of autosexing breeds depends upon the fact that males are *BB* and females *Bb* (see Chapter Seven).

In most families of mice albinism is recessive. In chinchilla mice the heterozygotes, *Cc*, are intermediate in colour, and I succeeded in making albinism dominant by substituting *pp* for *PP* in a strain of chinchilla mice.

NOTES

In this chapter there may well be an element of somewhat deceptive over-simplification. Everything sounds just a trifle too straightforward and easy. One—two—three—four—success is at the breeder's door! Hagedoorn, however, was writing for breeders, not for scientists, and in any language the alphabet must be learned before the book can be read.

Chapter Five

Variation

All animals vary, no two animals being ever wholly alike. The causes of variability are many, but they can be roughly divided into two groups, causes that influence the development of the animals from without and inborn causes of difference.

The commonest cause of variation is age. When in a group some animals are very old, some are new-born, and others are of various ages in between, this cause alone produces a very great amount of variation. Animals of the same age and sex in one group, however, may differ considerably among themselves. This variation may be partly due to the variable influence of different factors that contributed to the development of the animals. Some animals may have been born in large litters, and others in small, some may have had better care than others, some may have been born in an unfavourable spot, or under unfavourable circumstances. Some animals in the group may be healthy, and others may be parasitized. Some may have been used for breeding at an earlier age than others.

Apart from these environmental factors in development, the inherited make-up of the animals of a group may differ. In a group of hens, some may be white and others black, some pigs in a litter may have standing and some may have drooping ears. Some sheep in a fold may be polled and others may have horns. In those instances we know that inherited differences, differences in the presence or absence of inherited developmental factors, are responsible for the variation.

Very often both groups of influences will have an effect on the same qualities. Differences in egg size in a flock of pullets may be partly due to inherited factors, but we know that the

date of hatching and the quality of the food also influence egg size considerably.

The amount of milk a cow produces is partly influenced by her age, and by feeding and care, all non-inherited developmental factors, but partly by inherited factors transmitted from the parents to the offspring.

By a study of variation as such we are never able to find out which part of the variation is certainly due to environment and which to heredity; yet it is extremely important for every breeder to know that the effects of those two groups of causes of variation are wholly different.

When we have a group of animals differing in quality, a flock of hens differing in laying capacity, a group of cows differing in milk yield, a herd of swine differing in general conformation, we may easily be led to believe that those animals are the best to keep for breeding which most fully conform to our standard of perfection.

This, however, is only partly true—for whereas the differences due to presence or absence of inherited factors can be used as a basis for selection, the differences due to environmental influence cannot be so used, they only tend to confuse the issue.

Two animals that differ in inherited make-up, and of which one has inherited a certain factor more than the other one, will also differ in hereditary quality. The animal that has inherited the factor will transmit it to its progeny, the other one will never do this.

The effect of environmental influences is wholly restricted to the individual. When we compare two bulls, of which one is a young vigorous animal, and the other a feeble fifteen-year-old bull, the former will not necessarily transmit his vigour, nor the aged one his weakness: for all we know, things may be the other way round. When we succeed in building up a bull for the shows, so that his back-line is just perfect and he has fat in all the correct places, but no bulk where he is supposed to be slim, this does not help him in getting any more perfectly formed young stock.

In the breeding of sugar-beets we have an excellent example that illustrates this point. The beet-seed specialist will select his groups for high productivity, and when he has obtained some excellent breeding stock, he must multiply this stock in order to

sell seed. To save space he sows the seed very thickly, so that he harvests a crop of miserably thin scraggy beets, which are wintered and planted in spring at suitable distances to grow a crop of seed. The fact that these seed-bearers have no value as individuals does not impair their value as parents of commercial beets; the essential point is that they have a valuable hereditary make-up, and this is what is inherited.

It seems so evident that in a group of animals the most perfect ones are likely to have the best offspring, that many breeders think they are doing all they can do when they continually weed out poor specimens and keep only the very best animals for reproduction.

Once we realize that an animal's qualities are as much due to environmental influences as to genotype, it becomes evident that the ordinary variability, which we can witness in any group of animals, is partly due to heredity and partly to other influences.

In any flock of hens the birds will vary in number of eggs produced; and some hens will have better daughters than others. At first sight it would appear that the best-laying hens must be those that have the best daughters, but this is far from true. If we could have an absolutely pure breed of poultry, in which no genetical variability existed, and in which therefore all hens had absolutely the same genetical make-up, the number of eggs produced by the pullets would still vary from individual to individual, but the poorest layers would be just as good for breeding purposes as the best ones.

Breeders as a rule over-estimate the part played by heredity in variation, and under-estimate the rôle of environmental causes of differences in their stock. Repeatedly we find that fanciers, when establishing a scale of points to judge their animals by, at the shows, or at the time of stud-book registration, attach great value to characters that are subject to great influence by the environment. In almost all scales of points established by cattle herd-book, points for "back" and for "loins" take up a considerable part of the total points. It is very surprising when one finds that the difference between an animal that is especially strong on those points and one that fails in them is chiefly caused by suitable feeding or the reverse.

We can get a rough idea of the relative parts played by heredity and by environment in the variation of our animals by

two means. It is obvious to experienced exhibitors and judges that very much can be done to improve an animal's appearance by feeding and training down to trimming, massaging and faking. When our judges get into the habit of admiring animals of fine appearance, this soon leads to a state of things where bulls and stallions must be shown rolling fat, and where differences in this sort of "constitution" completely hide other differences due to heredity.

Another means to get an idea about what is due to inheritance and what to environment, is to study the correlation between parents and offspring in regard to different points. When we find that in a black-and-white breed of cattle the bulls with much white on the average have daughters with more white than the very black bulls, this shows that the amount of white in the coat is largely due to inherited factors. If, on the other hand, we find that the bulls with the highest points for "Back and loins" have daughters that do not average any higher in these points than those of bulls with low points for these items, we know that quality on those points is mostly due to environmental influence.

In scientific genetic publications we generally reserve the term "variation" for the influence of genetic factors, while using "modification" for the influence of environmental factors. In most instances variation is found to be continuous, that is to say, if we arrange a series of animals according to any quality, we find that the differences between them are gradual. The larger the number of animals we examine, the better the gaps are filled in, so that in a very large number almost all gradations are found.

This is not always true: sometimes we find instances of discontinuous variation, where in a series of animals sudden breaks occur.

Discontinuous variation is found in all instances in which a factor in the development has a very great influence, and such a factor may be either an inherited factor, a gene, or an environmental influence.

In canaries, examination of a mixed group always shows that the birds are either crested or plainheads; in the development of crest we see the influence of one gene very clearly. Within the group of crested birds, the crests may again vary continuously. In cattle and sheep size of horns may vary continuously,

but one gene produces the difference between horned and polled animals—here variation is discontinuous.

Continuous variation is often due to the interaction of a great many genes, for which the group is not pure: but this does not mean that, wherever we see continuous variation, a large number of inherited factors are concerned. In fat content of milk we see all gradations in a herd of cows, but it is very possible that only one or two genes are really concerned, and that we have so many gradations because environmental influences modify the character.

The most striking instances of variation are those in which animals with unexpected novel characters suddenly turn up. In the domestic animals such cases are frequently found, most of them on examination proving to be due to the cropping up of individuals that lack one or more genes.

The cause of such unexpected "sports" may be mutation, that is the spontaneous loss of a gene from some germ-cell, mostly in an ancestor some generations removed. In such an event the mutation may result in the production of a heterozygote, which breeds some more heterozygotes, and later, when two heterozygotes happen to mate, the individuals with the novel character originate.

The most frequent cause of the origin of such sports, however, is cross-breeding. Cross-breeding always results in the production of animals that are heterozygous for all the factors in which the parent breeds differ. If we breed from the hybrids, in every case only three out of four of the young will get such a gene and one will be without it.

It often happens that in two breeds a very similar but different gene is present, each of which has about the same effect on development. If this happens, one-fourth of the young animals will lack one of those factors, one-fourth of all will lack the other one, so that in all, one animal out of sixteen will have neither the one nor the other.

In our own cross-breeding experiments with rats we met several such instances. If in one species the animals are grey instead of yellow, because they have a factor *A* (but not *B*), whereas in the other species *B* is present (but *A* is lacking), the hybrids will have both *A* and *B*, but they will be heterozygous for both (*AaBb*). Such hybrids, when mated together, will have a very few (one in sixteen) young that lack both *A* and *B*. Their

formula in respect to those two genes is *ab*, and such animals are yellow.

The production of such double recessive novelties is a very common thing, wherever different breeds are crossed.

It sometimes happens that a striking character is due, not to the genotype of the individual showing it, but to that of some other individual.

In a recent case we found in one family some mice without whiskers. It could be shown that the absence of whiskers was due to an inherited tendency of some mice to eat their companions' whiskers (they could not eat their own).

The mice with the inherited aberration looked normal; their barefaced companions were simply victims, and not genotypically aberrant.

When two apparently very similar breeds are crossed, it is possible that those breeds do not have the same hereditary make-up. In such instances new unexpected (often quite unpleasant) qualities will be shown by some of the second-generation progeny. The crossing of two breeds generally leads to a very great variation. When it is deemed advisable to ameliorate a breed, crossing it with a similar breed may cause the sort of variation we can use in our selection work; but crossing two breeds should never be loosely undertaken, as it will tend to destroy the painstaking selection work of many years and create an enormous amount of unwanted variability and impurity.

Geneticists have learned very many things about variation, its causes, and the way it can be controlled. The animal-breeding industry is only just beginning to realize the importance of this mass of knowledge for animal breeding. The success or otherwise of different methods of selection in different cases hinges upon the sort of variability present in the material.

On this point geneticists who are studying variability and heredity can be of the greatest help to animal breeding if they will take the trouble to use their knowledge in a critique of animal-breeding methods. Where breeders use inadequate or wholly worthless methods, the reason is almost invariably found to be a misapprehension of the variation with which they are dealing and its causes.

NOTES

This is a very clear and extremely fair statement of the causes of variation in farm animals. Although by training and profession a geneticist, Hagedoorn makes no attempt to underestimate the power of environment in producing variation although, of course, emphasizing the hypothesis which he regarded as fully proven, that such variation environmentally produced is under no circumstances heritable. His statement that: "Breeders as a rule over-estimate the part played by heredity in variation, and under-estimate the rôle of environmental causes of differences in their stock", is one which I can fully confirm from my personal experience. When working at the Rowett Institute I frequently had to demonstrate sheep-feeding experiments to parties of farmers. The difference resulting from a quite simple alteration in diet, such as a vitamin or mineral deficiency, is often quite dramatic. Many farmers were adamant that the sheep at the beginning of the experiment must have been quite differently bred. It was hard to convince these farmers that it was not so. Some of them were never convinced. I am inclined to go further and to suggest that the importance of breeding in animal husbandry has been considerably exaggerated not only by breeders but by most other people concerned with the subject. Hagedoorn, being a geneticist, could hardly have been expected to subscribe to that view.

Two minor statements in this Chapter seem to me to require critical comment. Discussing the fat content of milk, Hagedoorn suggests that ". . . it is very possible that only one or two genes are really concerned". I doubt whether any other modern geneticist would accept such a suggestion.

In another passage Hagedoorn writes that, "The crossing of two breeds generally leads to a very great variation." This statement seems to contradict subsequent passages in later chapters emphasizing the uniformity resulting from the first cross between two breeds. I imagine, therefore, that what Hagedoorn is referring to here is the variation which occurs when the first-cross progeny between two breeds are themselves interbred.

Chapter Six

Selection

The aim of selection is to make the animals and birds of the next generation as good as, or better than, those of the present one. It is very generally believed that our present breeds of domestic animals have been slowly evolved from the breeds that have gone before, and ultimately from wild ancestors, by a process of selection.

The idea that selection must certainly be effective, that every time we choose animals that differ in some way from the average quality of a group in which we find them, in order to breed the next generation, then this next generation will be found to be shifted in that same direction, is extremely prevalent. It is based upon a belief in the inheritance of the qualities of animals and plants.

When we think the qualities of an animal are somehow passed on to its progeny, it seems obvious than those animals that have some quality to a high degree will certainly have offspring that will be more extreme in that point than the general population. To give an example: if we see that the birds in a breed of poultry vary in size if we weigh or measure them carefully, it seems evident that when we select the smallest pair of birds in each generation, and keep up this selection, the birds in our selected line will get smaller and smaller regularly, until finally we have reduced them to a bantam-replica of the breed with which we started.

It must come as a shock to some breeders to learn that on the whole those ideas are not true. It is certainly impossible to make bantams out of a large breed by straight selection. The fact is that the supposition on which those ideas are founded does not hold. The qualities of an individual are not inherited as such.

The only things that are passed from parent to offspring are material substances in the cells, the genes, which certainly help to give the developing animal certain qualities, but which are by no means to be looked upon as the sole causes of the "inherited" characters.

The qualities of an organism are partly due to a great many different co-operating environmental causes, and as these factors affect only the development of such an individual, they are not inherited, and neither are their effects. In fact, most of those non-inherited factors are of such a nature (temperature, food, forces) that their action is exerted only at a certain stage of the development of the parent, so that any inheritance effect is wholly excluded. Drought during spring may stunt a plant, but it would be very difficult even to imagine how this temporary action of drought, resulting in a permanently small stature in this plant, could ever affect the size of the daughter plant growing from seed produced by the stunted parent.

For this reason selection can only be effective inasmuch as the group of organisms, chosen to be the parents of the next generation, is found to differ genetically from the general run of organisms in the group in which we made our choice. In other words, genetic variation is the sole basis for effective selection.

To be effective, selection must set apart a group of organisms that differ genetically from the average in the group from which we select them.

To return to our example; in a breed of poultry, part of the variation in size may indeed be due to inherited factors, in respect to which the breed is not pure. In so far as this is true, selection may indeed produce a group of smallish birds; in fact, when we find the right means of doing it, we might produce a group in which the birds all had the best possible combination of genes consistent with small size. In the end this would give us a smaller breed, with a smaller average size, but as soon as the most favourable combination of the available genes is reached, a limit is set to further improvement.

When we realize that selection can have results only if it separates individuals or groups that differ in inheritance, in genotype, it becomes easier to understand why straight selection sometimes has much more effect than in other instances.

In order to produce a certain result by straight selection of a group of organisms, we must find a way to recognize such in-

dividuals. This is much easier in some instances than in others. If the difference between the average individuals of a group and the few we like is caused by the presence or absence of one or two genes that have a striking effect, selection may be very effective. Some genes have such an important rôle in development that their absence causes a very striking difference. If we find a few albinos in a group of animals, selection of a small group of such aberrant animals mostly produces an albino breed at one step. When in a breed of cattle we choose a small herd of red ones from among the prevalent blacks, we produce a red sub-breed right away. This has been done in Friesland. In some groups of animals and birds, the only breeds ever produced are breeds that have originated in such a way. The white peacock, the dark-golden pheasant, the black and the albino rat are examples.

The first complication, which makes plain selection for individual quality less effective, is caused by dominance. It is very easy to make a red sub-breed of cattle when a mixture of reds and blacks is given; but to produce a pure-breeding race of black cattle from such a mixture by plain selection is far less easy, for the simple reason that some black ones are pure and some are heterozygous; in respect to the one inherited factor blacks have more than reds. To make a pure-breeding group of blacks, we would have to select a few homozygotes, but as those homozygotes do not differ in colour from heterozygotes, plain selection according to colour is not as effective as we should like it to be. In many black breeds of cattle a considerable proportion of heterozygotes is always present, and ordinary selection for black colour, that is the constant rejection of red calves, has not been able to rid the breed of the impurity.

When in such circumstances we begin selecting, progress may be rather rapid, but when a certain limit is reached, progress slows down considerably. When in our example we started from a herd in which the reds were as numerous as the black animals, selection of a group consisting of black ones only would give us a herd in which the great majority of calves born would always be black; but getting rid of the reds entirely is a very difficult problem.

So far we have discussed examples in which the result of the action of an inherited developmental factor was striking, much greater than any environmental influence upon the character:

but such instances are really exceptions. Most qualities of our domestic animals are influenced both by environmental and by inherited factors. Such characters as size, weight, milk yield in cattle, and egg production in poultry, certainly vary both because of inherited differences between individuals and owing to environmental influences.

This produces a very great difficulty, which may in certain instances be so great as to make the effect of straight selection for individual merit very ineffective. This is so because, for example, birds that show great merit may do so either because they have an excellent inherited make-up (in spite of adverse environment), or because they were very favourably influenced by environmental factors (while of mediocre inherited quality).

If we want to give an illustration of this difficulty, we can do it by representing merit in an individual by the height of a column, part of which is shaded and represents the effect of the environment, and part of which is black and represents the genotype which affects the quality.

When both the effect of the environment and the genotype vary, individual merit, which is due to the sum of both components, gives no good indication of inherited quality.

It may sometimes be possible that the inherited make-up of all the individuals is alike (Fig. 3) and variation in merit is wholly due to environmental influences. Here selection of the best individuals has no effect whatever.

One of the best ways to make straight selection for individual quality effective is to keep the conditions under which the individuals live as constant as possible. In Fig. 3 we see that when the environmental influences are alike in all cases, the final quality gives a correct picture of inherited make-up, with the exception that dominance can still complicate things. In breeding practice, however, this is exceedingly difficult, because so many non-inherited influences have much more influence on the final result than we imagine. This makes special methods of selection necessary.

From the above it is evident that the importance of plain selection based upon individual merit (phenotype) is not very great, except in very special instances or circumstances. Part of the belief animal breeders still have in this system of selection is certainly due to the influence of Darwin's views on natural and artificial selection. Before we knew that two fundamentally

different sets of causes always influence the final quality of an organism, it was universally believed that the qualities of an organism influenced the quality of its germ-cells and so the quality of its offspring.

Earlier generations of naturalists believed that under the

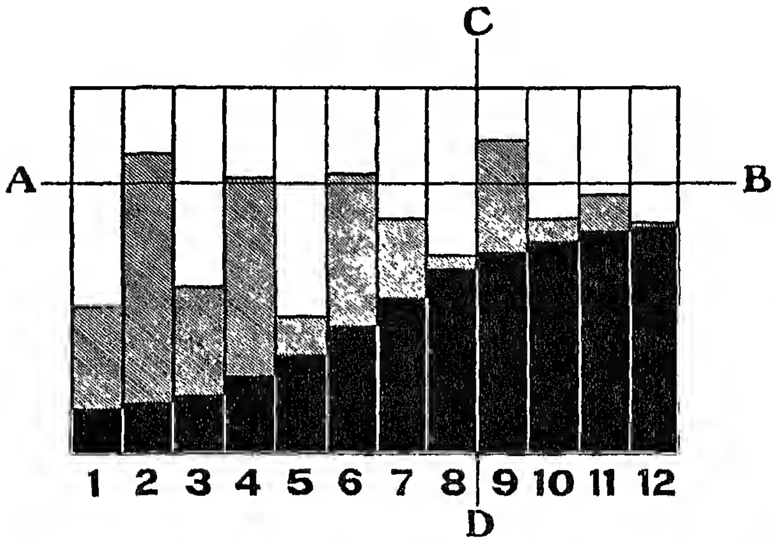


FIG. 3.—Diagram showing the difference between genotype and phenotype as a basis for selection. The height of the black part of each column (which represents an individual) represents the part played by the inherited make-up in the development of the character appreciated. The cross-hatched part shows the part played by environmental (non-inherited) factors. The total height of each column shows the quality. Twelve individuals are arranged according to their genotype.

When we select the four individuals that show the character (phenotype) in the most perfect way, we select according to the line A–B, and the individuals selected are No.'s 2, 4, 6 and 9. When we select according to the best genotype, for instance by means of a progeny test, we select according to the line C–D, and we actually get the four individuals most valuable for breeding the next generation.

When we select first according to appearance, this group (2, 4, 6, 9) only contains one of the really good breeders. It is safer to select according to genotype from the very beginning.

influence of selection-pressure, every breed and every species in nature was slowly but surely changing.

Nowadays geneticists distinguish between variation, the effect of genotypic differences, and modification, the result of environmental influence. We know that the gross variation we see when we compare large groups of organisms is always produced by environmental modification superimposed upon genetic

variability: but as only the genetic differences are inherited, gross variation is very often a very poor basis for selection.

Another chapter treats of the causes for stability in existing species and domestic breeds. The more we begin to doubt the effectiveness of straight selection, and the more we study the effects of different systems of selection, the clearer it becomes that breeds of domestic animals, protected from cross-breeding, are relatively very stable units, upon which straight selection has very little effect. Breeders tend to underrate the influence of environmental and overrate the importance of inherited differences.

Most of the changes we see in our present animal breeds, and which are accompanied by constant selection, are not really caused by the selection at all, but by a substitution of one breed for another either by just plain substitution, or else by cross-breeding and grading. When breeders believe our present very productive dairy cattle have been produced by a process of straight selection from the sort of cattle kept in the same stables a century ago, they are generally mistaken. Such changes are usually produced by the repeated use of bulls belonging to a different family with a higher yield, when conditions of agriculture (imported feed and artificial manures) have made a higher-yielding breed more profitable.

In many instances selection-experiments show very little, if any, result. Sometimes this negative result is to be expected. When we found that fifty generations of straight selection in varieties of wheat had been ineffective to change any of the characters studied, this was easily understood, as we knew that in wheat self-fertilization rapidly produces complete purity for inherited factors, so that here the modifications on which selection had been working were wholly due to non-inherited effects of environmental conditions.

When I found that in a strain of mice selection for fertility was wholly ineffective, I knew that the strain with which I worked had been strictly inbred, brother to sister, for over thirty generations, so that genetic differences were probably absent.

When it was found, however, that ten generations of the strictest selection of the best-laying hens, mated to sons of the very best layers, had no effect at all, production after the selection being just a little bit lower than at the start (State of Maine Experiment Station), this result was very striking and un-

expected. It became very much more so when R. Pearl, continuing with the same material, could show that a better system of selection resulted in marked improvement.

Many poultry breeders use a system of selection based entirely upon individual merit. They mate the son of an excellent hen with a group of hens, each of which has been selected wholly upon high individual merit. This system has repeatedly been shown to be practically worthless. It is almost certain that the results would be just as good if no selection at all were attempted, but if males and females of good health were taken at random.

This primitive system of selection, which was almost universal twenty years ago, always results in a complete "reversion" of quality in every subsequent generation. The breeder finds that in every comparison between mothers and daughters, the quality of the daughters is always much below that of the mothers used for breeding. Poultry breeders have always taken this reversion to indicate the need of a continued process of selection, as they have thought the cause of the reversion is a tendency for poultry to degenerate. If a man finds that the daughters of his 250-egg hens average 200 eggs, he is convinced that if he used all those daughters, without selection, next generation his hens would drop to 150 eggs or thereabout.

The real situation, however, does not depend upon reversion at all. The daughters are not really less good than the mothers—they probably average just about the same as the mothers. The point lies in the inherited quality of the selected group of mothers. If the generation of hens to which the mothers belong average about 200 eggs, there is no real reason to believe that the few hens in that group which laid 250 eggs are different in inherited make-up from the rest of that lot. Their genotype is probably just the same as that of the 200-egg hens. If such a breeder chooses those hens as breeders, which lay only 175 eggs, their daughters will probably lay 200 eggs on the average, just as all the daughters of all the other groups of healthy hens chosen.

Plain selection on the basis of individual merit is not a method of animal breeding that can be generally recommended, unless the problem to be solved is one of the most extreme simplicity (monofactorial recessives, where the factor has a very great influence).

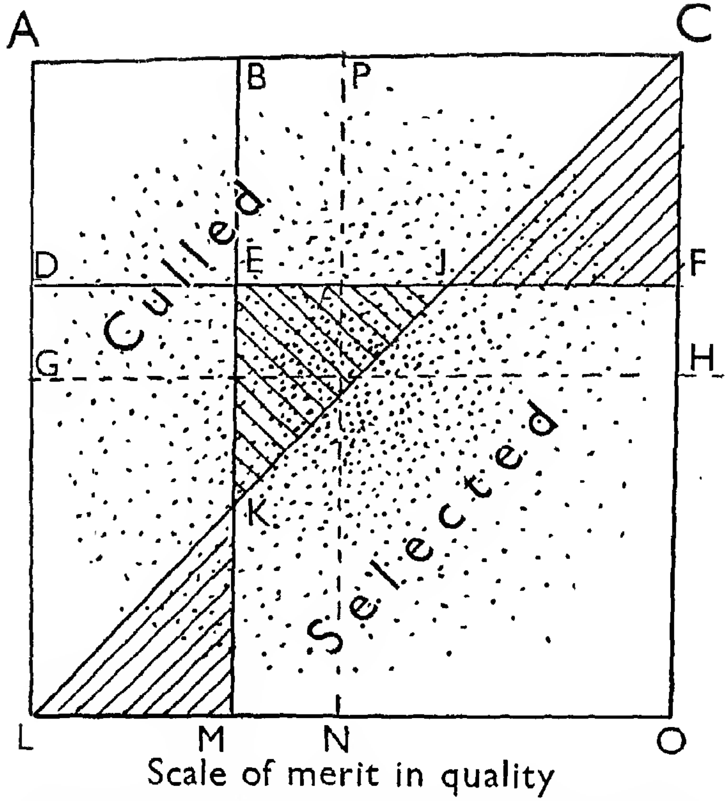


FIG. 4.—Superiority of selection on total score as compared with culling first for one quality and then for another. Diagram after one in J. L. Lush's book, *Animal Breeding Plans*. Each dot represents an individual, and merit in quality *x* is independent of merit in quality *y*. One half of the individuals must be culled. If we cull first for quality *x* and reject all the animals above line D–F, and then for quality *y*, rejecting all the animals to the left of B–M, we keep all the animals within E–F–M–O. If, however, we score each animal for both qualities *x* and *y*, we reject all the animals above the diagonal L–C and select all those below it.

Animals of outstanding merit in one respect, included in triangles J–C–F and L–K–M would be kept if selecting for total score, but rejected when culling first for one, then for the other quality. On the other hand, the individuals within triangle E–J–K, animals below the average, would be kept when culling first for one, then for the other quality, but in selecting for total score they would be culled.

In a good many instances, only the animals of one sex can be judged according to their individual merit, and in all these it is obvious that breeders who believe in personal merit as a basis of selection are up against a great difficulty. This difficulty has

given rise to several working methods, one of which is to use the qualities of one parent as an indication of the value of an animal whose personal merit cannot be directly determined. Poultry breeders often use a cockerel because his mother has laid a great many eggs; cattle breeders often believe that a bull, whose mother is an excellent milker, must be valuable as a sire.

If we test such methods according to the criterion given above, namely, that a method of selection can only be effective if it chooses the animals with the most valuable set of inherited factors, it is obvious that the quality of a female can never be used as a safe guarantee of the correct inherited make-up of her son. The quality of the mother in itself is no guarantee of her own heredity, and if we add the fact that each animal also has a father, of which we can never know just what he contributed to his son's make-up, the method must always remain extremely risky.

The difficulty of judging a male in a breed, where only females are kept for economic usefulness, has certainly contributed to a method of selection which consists of using as indicators of inherent quality characters that are thought to be correlated to the ones really sought. A special chapter is devoted to this method. As such correlated characters can never give us a picture of the inherited make-up of our animals, in so far as concerns genes that influence economic value, the method is extremely speculative and can never be recommended. In so far as correlations do not really exist between such secondary marks of value and real quality, the methods are apt to lead us astray. Where such correlations really exist, the method is superfluous.

As the aim of selection is the choosing of individuals that have the correct set of inherited factors, methods which seek to evaluate those factors themselves have been developed. In some instances it is possible, by means of deliberate test-matings, to find the genotype of an animal as far as one or two factors are concerned. Test-matings are dealt with in a special chapter. This is very dangerous ground, for the reason that it is easy to pay too much attention to one or two genetic factors one happens to know. The von Patow system of attributing genetic formulæ to bulls and cows, which are found by examining the milk yield and fat content of the milk in dairy cows, is a typical example of this method driven to its ultimate conclusion. Geneticists, I am glad to say, do not take this seriously.

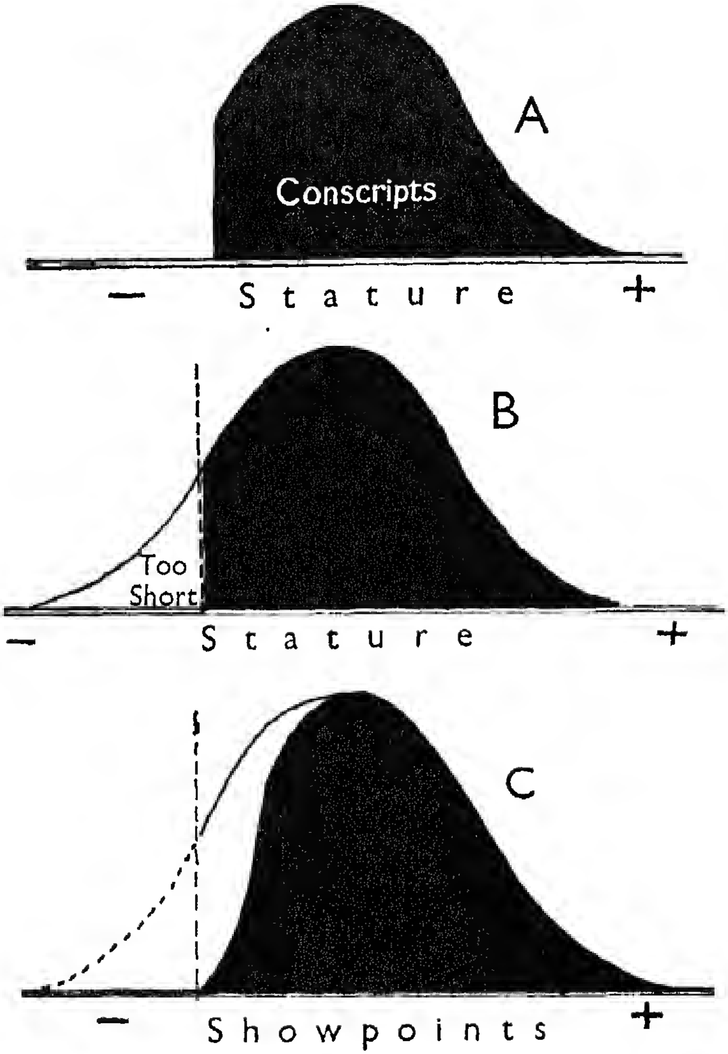


Fig. 5, a and b.—The peculiar shape of the variation curve showing stature in soldiers is caused by the circumstance that a number of recruits are rejected because they do not come up to the minimum height. This can be seen by comparing A with B, which denotes variation in stature in the group of recruits before selection has removed the undersized boys.

Fig. 5c.—Variation in total score in a herdbook where heifers are registered only after selection according to show points. Notwithstanding the fact that a great number of young females are rejected because their total score does not add up to 70 points, the variation curve in the registered group is fairly regular and lacks the peculiar shape of the curve in Fig. A. The shape of the curve clearly shows that in this instance the total score is not really made up by adding separate points

Every animal has its own genetic make-up: it is homozygous for a number of genes, heterozygous for others, and it lacks some genes that are present in its relatives. For these reasons it will breed in a certain way, and have offspring of a certain quality.

Now it is more important that we should be informed about the quality of an animal's offspring than that we should know what genes the animal possesses. Even if we had the means of finding out the genotype of the animal in respect to three or five important genes, we would know that this knowledge is very incomplete, as a dozen or a hundred other genes influence the qualities that interest us. For this reason it is much more important that we find out in which way an animal breeds than how its genotype is in respect to a few genes.

The safest way of judging the value of an animal as a breeder is to defer this judgment until after it has bred, and to judge it accordingly. After all, this is the only method of selection that does not depend upon speculation or theory. In the special chapter on progeny-testing I have gone more deeply into this subject, and have tried to prove that wherever we use this method, we must use it to the exclusion of more speculative tests, such as the selection according to correlative characters.

In plant breeding, methods of selection have gradually been simplified and rationalized, so that many speculative or ineffective methods have disappeared completely. In animal breeding we are just now passing through a period in which breeders are beginning to realize the importance of genetic critique in matters of working methods. Many thoroughly irrational systems of selection are still being used by animal breeders, and the main object of this book is to help the breeders to substitute rational systems of selection for wasteful ones.

for horns, back, loins, etc., but that the judges unconsciously make up the score to fit their impression that a given heifer must be registered or rejected. If the whole group of females was really judged objectively according to the number of points, the variation curve would probably look as indicated by the dotted line.

(See revision of diagrams in Appendix on pp. 359, 360, 361.)

NOTES

Selection is probably the most important tool of the breeder of farm animals. This chapter of Hagedoorn's impresses me as being an excellent introduction to the subject, clearly worded and fairly put, worthy of careful study by all breeders.

Apart altogether from genetical considerations, its main conclusions are incontestable. Thus, Hagedoorn wrote:

"Many thoroughly irrational systems of selection are still being used by animal breeders . . ." Is there anyone having any practical knowledge of the business who could deny that accusation? The difficulty is to design alternative systems that are entirely rational. That difficulty, to me, seems much greater than the majority of geneticists are prepared to admit. I have heard geneticists advocate changing the genotype of a breed to suit economic purposes by selection as though genes were coinage and heredity a till. Actually, the problem is far more complex.

I agree entirely with Hagedoorn when he wrote that:

"Most of the changes we see in our present animal breeds, and which are accompanied by constant selection, are not really caused by the selection at all . . ."

That is a bold statement for anyone, let alone a geneticist, to make, yet I am sure it is a true one. Take selection for higher milk yields in dairy cows as an easily followed example. It is a simple matter to show that in every country where agriculture has become intensive, the average milk yield of dairy cattle has shown a substantial increase within historical times. This increase in milk yield is attributed almost universally, but nevertheless somewhat uncritically, to the influence of selective breeding for higher milk yields over the same period. Yet, is this really so?

As Hagedoorn wrote:

"The primitive system of selection, which was almost universal twenty years ago, always results in a complete reversion of quality in every subsequent generation."

It is difficult to imagine how it could have been otherwise. Until recently, almost universally, and to a large extent even to-day, selection is based on the milk yield of individual cows which is only slightly heritable, and on conventional judgments of dairy bulls which may have no relation to milk yields whatsoever.

If Hagedoorn's statement be true—as I believe it to be true—that the "system of selection, which was almost universal twenty years ago" was ineffective, how can it be maintained logically that such ineffective methods of selection led to higher milk yields?

My own view is that the higher average milk yields of to-day compared with those of, say, a century ago, have resulted from general advances in husbandry, both crop and animal, to the better feeding and housing of cows, to advances

in veterinary science leading to more effective control of disease, and that selective methods of breeding, whether effective or ineffective, have had very much less to do with the matter than is generally supposed.

I don't think for a moment that Hagedoorn would have gone quite as far as that. Being by training a geneticist, it was perhaps inevitable that he should stress the importance of the breeding factor in animal production. Yet, he was never a mere theoretician. Hence, the unquestionable common sense of one of his final statements concerning selection.

"The safest way of judging the value of an animal as a breeder is to defer this judgment until after it has bred, and to judge it accordingly. After all, this is the only method of selection that does not depend upon speculation or theory."

Chapter Seven

Inheritance of Sex

In all our domestic animals and birds, the sex ratio is approximately equality. This observation, coupled with facts of sex-linked inheritance, led to the hypothesis that in every species one of the sexes would be heterozygotic for something for which the other sex was thought to be homozygotic. When the cytology of the chromosomes developed, it was found that this something is not one gene, but a complete chromosome.

In some animals, the male sex is heterogametic, and the female sex homogametic. This means that in the cells of the males, one chromosome is single, while all the others are double, whereas in the females all the cells have a complete double set of chromosomes.

In other animals, however, the reverse is true, the female sex being heterogametic. This is so in butterflies and in birds, whereas in mammals the males are heterogametic.

This means that, in respect to all the genes carried on the unpaired sex chromosome, the female in birds or the male in mammals must necessarily be heterozygous. The other sex, however, may be either homozygous or heterozygous. Of course it may so happen that animals of either sex lack the gene in question altogether.

This situation leads to some remarkable consequences. We must look upon all the specially male or female qualities as primarily caused by a difference between one and two doses of genes on this chromosome.

When we mate a female bird to a male that lacks one of the genes the female carries on the sex chromosome, half of the offspring will have this gene, and the others will lack it. As, however, the birds into which the sex chromosomes enter will

become males, this means that in such circumstances the males will show the character of the mother and vice versa. This results in criss-cross inheritance, which is sometimes made use of when it is important to recognize the sex at birth in organisms where this is otherwise difficult.

The first cases of this criss-cross inheritance studied were those in which the phenomenon was used commercially. Around the town of Assendelft in Holland, in Egypt according to Mr. Doorenbos, and in the Belgian Kempen, poultry farmers used to mate female silver hens to golden cocks, and they would get yellow chicks (all females) which they raised for egg laying, and white chicks (males) which were killed at birth. Sometimes the cockerels were not killed, and in the Halles in Paris large numbers of flat boxes of baby chicks used to be offered for sale, imported from Belgium, every chick later proving to be a male.

When around 1905, I gathered data about the breeding of Assendelvers, I found the following data:

Parents	*Progeny*
Golden male, silver female	—Golden females, silver males
Golden male, golden female	—Golden females, golden males
Silver male, silver female	—Golden females, silver females, silver males
Silver male, golden female	—Golden females, golden males, silver females, silver males

In England especially, the production of so-called sex-linked chicks, produced as hybrids between different breeds, has become quite an industry, under the guidance of Professor Punnett. The most usual cross is that between Rhode Island Red males and Light Sussex females, which cross gives silver males and golden females.

In working with the "barring" factor, Punnett and Pease discovered that this factor, which is also carried in the sex chromosome, has such an influence upon brown-downed chicks that the sexes of pure-bred chicks can be distinguished, as in such a breed the homozygotes (males) can be distinguished from the heterozygotes (females). They produced the "Cambar" by breeding this barring factor into a strain of Brown Campines.

As, however, this breed has very little commercial value, it was necessary to do the same thing for commercially valuable brown-downed breeds. By crossing the Brown Leghorn and the

Brown Barnevelder each with a breed containing the barring factor and often repeated back-crosses, I have succeeded in making an autosexing Barnevelder.

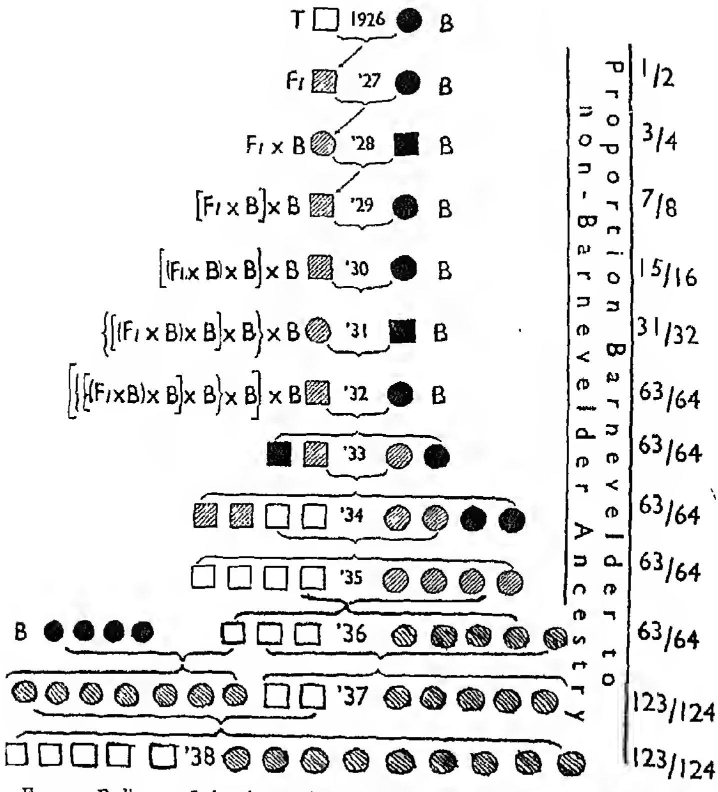


FIG. 7.—Pedigree of the Autosexing Barnevelders. Squares stand for males, circles for females. The birds of the present generation have one non-Barnevelder ancestor, eleven generations ago, from which the "barring" gene has been derived. White figures denote birds homozygous for the barring factor (AA), cross-hatched figures stand for heterozygotes (Aa or Ao), and black figures denote non-barred birds. After six back-crosses a few homozygous (AA) males were produced by mating heterozygotes *inter se*, after which the breed was practically pure. A further introduction of pure Barnevelder females was made in 1936.

The autosexing Barnevelder was made by breeding birds containing the barring factor eight times back to pure Barnevelder. The males in this breed are barred, with red in the wingbows; the females are almost as brown as ordinary Barnevelders. The

chicks are born in two colours, whitish males and brown females.

During the second world war we finished making the auto-sexing Rhode Island Reds. In this breed the cockerels are born white and the pullets buff. In the adult birds the males are red and white barred, the females are very little different from ordinary Rhode Island Reds.

In this breed, therefore, barring is recessive, whereas in the autosexing Barnevelder it is intermediate, and in such breeds as the Barred Rocks barring is a dominant character.

I am firmly of the opinion that in future the autosexing breeds will be of great economic importance, as many poultry-men prefer to keep just one breed, and still want to have the possibility of quickly distinguishing between the sexes of the newly-hatched chicks. The so-called "sexing" of baby chicks by experts, examining the vent, which is quite easy in ducklings, takes time; the breeding of autosexing breeds saves an enormous amount of time to the hatcherymen.

NOTES

This chapter, although such a short one, is of particular interest from several points of view.

The mechanism of sex inheritance, with an exact agreement between the results of breeding experiments and cytological observation provides one of the strongest supports to Mendelian theory.

Perhaps just because of this, geneticists are inclined to exaggerate its importance in animal husbandry. Its main application has been to sex-linkage in poultry with a view to accurate sex determination of day-old chicks. In this case, as in many other animal husbandry techniques, practice preceded theory. Poultry breeders were sexing day-old chicks on the basis of down plumage before the Mendelian explanation of the mechanism was ever propounded. Hagedoorn cites several such interesting instances.

The establishment of auto-sexing poultry breeds—the Cambar of Punnett and Pease at Cambridge was the earliest example—while an interesting application of genetic theory, is of relatively minor economic significance since the auto-sexing breeds never seem to have attained any substantial degree of commercial importance.

In any case, the very different Japanese technique of vent examination has rendered sex differentiation by down plumage less essential. Hagedoorn's enthusiasm for auto-sexing breeds is one which hardly appears to be shared by the industry.

Chapter Eight

Domestication

When we remember that our present domestic animals and cultivated plants are not fit to live without man's protection, we are forced to the conclusion that our domestic animals are descended from wild species. When we notice the great similarity that exists between certain domestic animals and certain wild species, between the ferret and the fitch, between the alpaca and the vicuna, the dog and the wolf, it becomes evident that man has domesticated wild animals to make his present domestic stock. How do we have to picture this process?

When we did not know as much as we know at present about the causes of variation, it seemed quite simple to assume that a continued process of breeding animals in captivity will make domestic animals out of them. We know that in many species young individuals, caught at an age before they have acquired their fear of man, grow up quite fearless and tame, and it sounds reasonable when we assume that the young of such tamed animals will again be tame, so that by a repeated process of selection during many generations an originally wild species will be transformed into a domestic animal.

This plausible explanation, however, is not very likely to be the true one. The evidence of the zoological gardens, where many wild animals are bred in captivity, does not support it. When we raise a young animal belonging to a wild species in captivity and in close contact with human beings, it may become absolutely tame; but this does not mean that its young, born in captivity, will likewise be tame. There is considerable evidence, that for deer and foxes raised in captivity, this does not hold true. When we want to breed deer in captivity, in order

to sell tame specimens, we must take away all fawns at birth and raise them on the bottle, for the fawns left with the mother will be wild, even when this mother is quite tame. Tame foxes in cages will warn their cubs so often and so emphatically every time they dare approach the caretaker, of whom the tame parents may have no fear whatever, that they become perfectly wild at an age of about four weeks. The only way to make these cubs grow up friendly is to take them away at two or three weeks and raise them by hand.

In regard to our present subject, animals can be divided into tameable and untameable species. In tameable animals, such as foxes and wolves, most carnivora, all the ruminants and swine, there seems to be no genotypic difference between domestic breeds and wild animals in tameability. In those species, young animals taken in hand early enough become tame, but even when the adults lose their contact with man, they are apt to become quite wild. Your pet horse may, when he gets in touch with a troop of wild ponies, be as wild as the rest in a few hours, and when you succeed in catching him again he will be as docile as before. In such species suitable methods of breaking and taming will make a tame animal out of a wild one in a very short time. In all these animals no inherited difference in tameability exists between wild ones and domestic ones; the fact that even the wild-born animals have a constitution which makes them tractable when suitably handled made it unnecessary to select for tameness during the process of domestication.

Some groups of animals, however, are untameable. Most rodents are in this class. We have considerable experience with rats and mice, and we have tried repeatedly to tame specimens of the black rat, or the small Oriental rat (*Mus concolor*), by giving them to tame rats to foster and handling them repeatedly, but all to no effect. Wild rabbits, even when fostered by tame does, are wild from the very beginning, and stay wild. In these rodents the domestic breeds differ from the wild related species in their inherited make-up, so that they are readily tameable. Domestic rabbits, rats and guinea-pigs are tame from birth, and remain tameable, even if they are raised without contact with man during several generations.

It would seem, therefore, that the breeding of wild species in captivity during a number of generations would not make domestic animals out of them. Under the influence of Lamarck,

Geoffroy St. Hilaire in Paris founded the Jardin d'Acclimatation in Paris in the middle of last century. It was proposed to produce numerous useful new domestic animals and cultivated plants by breeding suitable wild species under domestication for a number of generations. As far as animals are concerned, this object has been completely defeated, and no new animal has been added to the list as the result of these experiments.

We now know why this experiment was bound to fail. Domestic animals differ from wild species in their genotype, in their inherited constitution, so that we have to have material which varies in genotype before we can change it by selection.

The only cases I know in which domestic animals have been produced from wild species have been two very similar cases of the production of domestic breeds of rats in our own cross-breeding experiments with those animals. I will describe those experiments in detail.

We have bred the black rat (*Epimys rattus*) in cages for several generations without ever being able to get one tame. The same can be said for the Alexandrine species (*Epimys alexandrinum* and *E. tectorum*). In our cross-breeding experiments we made some complicated hybrids, by crossing *rattus* to hybrids between *alexandrinum* and *tectorum*. From these hybrids a large second generation was raised, which was extremely variable. Many novel characters were found in those rats, such as waltzing, yellow colour, silvering, white tail-tips. A strain of yellow rats was raised for some generations in cages, and by a process of partly unconscious selection, by the fact that some pairs were easier to breed in relatively small cages than others and were more easily tamed, we finally produced a strain of tame yellow rats, a real domestic animal. Exactly the same thing happened in California, when we tried breeding the Javanese and the Sumatra field rats (*Epimys diardii*) in cages. In neither case did we succeed in taming the animals; they were as wild and intractable after four generations of cage breeding as before.

At the same time, however, we raised some hybrids between the two strains. These hybrids were as wild as the rest, but they produced a very variable second generation. In this generation we found some albinos, and we also produced some waltzers, of two genotypically different kinds. Just as with the house rats, in the end we owned a strain of perfectly tame albino waltzing rats,

real domestic animals that were produced by cross-breeding and subsequent selection.

Now, it is perfectly possible for anyone working in a zoological garden to hybridize some wild species, and then, by a process of selection between the animals of the second and subsequent generations, to produce domestic animals from the lot. When, however, we think of the production of our present domestic animals by our human ancestors, it becomes evident that the production of domestic animals from the hybrids between several species, in themselves untameable, was out of the question.

When we review the present groups of domestic animals, we see the significant fact that in every group there exist wild related species that have a genotype that makes them tameable.

We will have to picture the process of the origin of domestic animals in some such way as this: A number of young animals of a tameable species are kept as pets and bred in captivity. Cross-breeding with a related species makes the group variable, and unconscious selection of the groups that are most useful or that show the most pleasing or striking new characters produces the novel domestic animal group.

Our common wild mallard (*Anas boschas*) is perfectly tameable. It is being bred in captivity and semi-captivity in different places, and the hybrids this duck produces when crossed with the pintail and other related species are perfectly fertile, so that we can easily imagine how, as a result of selection after species-crossing, our domestic ducks have originated.

The position with regard to domestic poultry is slightly different. Darwin, arguing from anatomic resemblances, thought that the red jungle-fowl (*Gallus ferrugineus*) must be the common ancestor of all our breeds of domestic poultry. There is, however, a very great difficulty here. From personal experience I know this species of jungle-fowl to have a disposition which makes it almost impossible to consider it as the ancestor to be domesticated first. Chicks of this species, even when hatched and reared by common tame hens, are exceedingly wild, and they will not stay around the house like domestic chicks. The only wild species of fowl that is tameable is *Gallus Soeneratti*, the chicks of which can be given as much liberty as tame chickens and they do not stray away. For this reason it is likely that individuals of this species were the first ones to be taken into cultivation. When

a group of tame *Soeneratti* fowls have been taken into a country where *Gallus varius* or *Gallus ferrugineus* occur, hybrids may have been produced which were responsible for most of the enormous variability that has given rise to all the different breeds of domestic poultry.

Oriental people take great interest in fancy poultry; charcoal burners in Java used to take a few hens of domestic poultry up into the mountains in the hope of breeding some hybrids from them with *G. varius* males. Hybrids between the three species of jungle-fowls named are sufficiently fertile to make it possible that a very variable second and third generation of the species-hybrids is raised.

The case of the rabbit is a very curious one. The wild rabbit is not tameable, but the hare is, and the hybrids between hare and rabbit are perfectly tameable. The history of the breeding of tame rabbits in France traces back to the production of leporids. Hybrids between hare and rabbit are perfectly fertile, and it is clear that we must think of this cross as the origin of our domestic breeds of rabbits.

In swine we have the same story, with the exception that all the wild species of swine I happen to know are tameable. Cross-breeding between European and Asiatic species may have produced the variability that made the production of domestic swine possible.

In cattle we have the difficulty that wild species closely related to our domestic breeds are not now to be found anywhere. It is probable that they have disappeared by being absorbed into the herds of domestic animals, in the same way in which the small herds of wild caribou now living in Alaska are being absorbed into the vast herds of tame reindeer that have been introduced in recent times into that country. It has been shown that species-crosses between our present domestic cattle and the banteng and some of the other Oriental species, are perfectly fertile, so that we are fully justified in assuming species-crossing as a source of the great variation we notice in domestic cattle. Yak × cattle and bison × cattle hybrids are fertile in the female sex only.

The facts regarding the horse and the donkey are very remarkable. Once in a while is produced a female mule that is fertile, and then the mare is fertile both with the stallion and with the donkey Jack. In America the "blood" of the donkey

has in this way been introduced into some breeds of horses, and reversely, horse "blood" has been introduced into the Jack-stock. It is evident that the enormous mule-like donkeys of Northern Spain may carry a considerable proportion of horse-genes.

The ferret has long been considered to be a domesticated fitch (polecat). It is true that the skull of the present ferret closely resembles that of the fitch, but this resemblance may have been due to cross-breeding with the fitch after the ferret was established as a domestic breed. From experience with the cage-bred fitch it seems to me almost impossible to believe that anybody would ever have thought of domesticating this animal. Even quite tame fitches are so quick and bold and snappy that the idea of going ferreting with a fitch sounds like going hunting with a pet tiger. It is probable that the original ferret was a domesticated Siberian fitch, a species that can readily be tamed and has a much quieter and more amiable disposition than our local black fitch.

There are a few domestic animals that are probably of monophyletic origin, namely the peacock and the guinea-fowl. The tame pea-fowl differ in nothing but in colour from their wild relatives, and it is possible that the present white and black shoulder and pied varieties have originated through loss-mutation, the loss of one gene in each instance.

The evidence of our own experiments with rats suggests that it would not be at all difficult to make real domestic animals from wild species provided we could find sets of two or three species that would produce fertile hybrids. The ideal of the Société d'Acclimatation could now be attained.

Our present domestic animals, however, fulfil a multitude of purposes, so that the number of novel, useful, domestic animals would be restricted to those categories of animals that nowadays are utilized as wild animals. Two groups of animals are now being utilized after being caught wild, a group of animals used as game, and a group of fur-bearing animals.

Among the fur-bearers, the only real domestic animal is the silver fox. Sometimes local sub-species such as the Canadian and the Alaskan silver foxes have been crossed, and from the resulting hybrids and their offspring have been bred strains of foxes that combine certain valuable characteristics, such as good quality of fur with good fertility in the cage.

It would be perfectly feasible to combine the excellent fur quality of the fitch with the fertility and other valuable characteristics, such as low food requirements, of the ferret.

It might be worth while to produce some new domestic animals in the group of animals now utilized as game. The introduction of genes of the domestic rabbit into the hare may easily make it possible to breed a strain of hares that could be profitably raised in hutches, and the same is true of some of the more valuable gamebirds.

Two new laboratory animals are now being bred in cages, the Syrian hamster and the Mexican cotton-rat. In neither of those species has it been possible to change the hereditary make-up. They are wild animals bred in captivity, and not yet domestic animals. The fact that in the case of the hamster all the stocks have been bred from a very few captured animals makes it probable that not sufficient hereditary variation can exist in the cage-bred material. Cross-breeding with different local species may be necessary before we succeed in making true domestic animals of this material.

Subspecies crosses in cotton-rats seem possible and might give us tameable strains as in house rats. In the 1950's, a few mutant hamsters were born.

NOTES

This is a chapter in which I find my views somewhat widely divergent from those of Hagedoorn.

He attempts to make what I regard as a too rigid division between species of animal that are capable of domestication and those that are not. He wrote: "In regard to our present subject"—i.e. domestication—"animals can be divided into tameable and untameable species."

It is certainly quite true to say that some species are much more readily tamed than are others but the distinction would seem to be one more of degree than one of kind. Possibly Hagedoorn, being a geneticist, tended to underestimate the importance of environmental factors both in initiating and in maintaining domestication. The degree of domestication seems to depend quite as much upon the closeness of symbiosis with mankind as upon the genotype of the species concerned. This is evident in certain breeds of hill cattle which tend to become unmanageable unless handled as calves.

Moreover, Hagedoorn, having divided animal species into the tameable and untameable, assumes that unless a wild species is readily tameable it cannot be

accepted as being the ancestor of a domestic species even though all other evidence points to the contrary. To me that seems false reasoning, indeed, argument in a circle.

It also seems to me that Hagedoorn over-stresses the importance of a polygenetic origin—i.e. descent from more than one species of wild animal—to explain the variability of domestic animals. He suggested a polygenetic origin of the domestic fowl as the explanation of its extreme variability. Yet the variability of the domestic dog is equally great although a monophyletic descent from one wild species, namely the wolf, is generally agreed. Perhaps it might be justifiable to suggest, as Darwin suggested, that domestication in itself induces variability even though the suggestion might be difficult to incorporate in present genetic theory.

Chapter Nine

Adaptation

Man lives in symbiosis with his domestic animals and his cultivated plants. This means that the relation is one of mutual interdependence. Man could not live without his animals and his plants; practically everything we eat, and almost everything we wear, is the product of cultivation.

Only in localities where very few men lead a scattered and precarious existence is it possible for them to exist without their own cultivated animals and plants, by eating and wearing what they can gather directly from nature.

In some instances the symbiosis-groups comprise only very few organisms. The Eskimo can exist with nothing but a dog; he lives in a region where animal life is plentiful and where man is scarce, and just a team of dogs to help him in his wanderings and in his hunts is enough for him. The Lapps only possess their reindeer and a dog to help them to drive these.

Generally, however, the symbiosis-groups are very complicated, and comprise both a number of animal species and a number of different cultivated plants. The relations between all these groups can be very complicated, but in general we can say that the cultivated plants produce more material, more seed, more tubers, as the case may be, than is necessary for the propagation of the species. Man harvests and saves some of the material for the next generation, and utilizes the surplus. Some of this surplus is eaten and employed directly by man, while some is used to feed his domestic animals. As these domestic animals under man's care also produce more young and more eggs or more milk than is necessary for the reproduction of their breed, man can utilize this surplus also for raiment or food.

Further, most of the domestic animals and cultivated plants

could not exist without man's care. They are dependent upon man's protection, and for this reason the relationship is one of mutual benefit, a true symbiosis. What is the nature of domestic animals and cultivated plants? We are not simply dealing with wild animals that have been bred in captivity, nor with wild species of plants that have been grown by man.

Many different definitions of the term "domestic animal" have been given, but few of them are satisfactory. We cannot say that domestic animals are different from wild animals in that they are tame, for there exist domestic animals that are not any tamer than their wild-living relatives. It is not true that domestic animals are especially tameable, for such essentially wild animals as the elephant and the wild boar have a disposition that makes them completely tame in suitable circumstances.

There is only one definition that fits all domestic animals, and it is the same that fits all cultivated plants. The races of cultivated organisms, namely, are fitted to live in symbiosis with mankind. They differ from related wild species and from the wild species from which they are descended in their inherited make-up, in some way which makes them useful to man, and sometimes also dependent upon man.

A few examples will suffice to demonstrate the correctness of this definition. Such animals as the ferret, the white rat, the white domesticated paddybird, differ from their wild relatives, from the fitch, the brown rat and the wild paddybird, in that their food requirements are more easily satisfied. The wild animals have food requirements, and especially vitamin requirements, which make it almost impossible to keep them in good health in captivity, and to make them reproduce in cages. Ferrets will reproduce on a diet consisting mainly of bread and milk, whereas the fitch would starve in a week on this diet.

The tame rabbit differs from its wild relative in the fact that young domestic rabbits are easily tameable, whereas young of the wild species are practically untameable. Among the many different adaptations of the dog to a life in symbiosis with man we find the very curious adaptation to mating dogs under human control, namely, a visible sign of a state of "heat" in females which is not present in the wolf or the fox, but which is equally possessed by another domestic carnivore, the ferret.

Whereas some of the domestic animals can be fed more cheaply than their wild relatives, some other domestic animals

are specially adapted to a very rich diet. Some of the better, highly-bred breeds of milk cattle and draught horses have the ability to consume great quantities of rich food and transform it into milk, or meat, or power. The egg production of our modern ducks and chickens is a very good example of the same thing.

In some instances the adaptation of the breed to human use is of a quite different kind. Some breeds of domestic animals differ from their wild relatives in psychic qualities, which are particularly useful. This is especially so in many different highly-specialized breeds of dogs—hunting dogs, watchdogs, herding dogs. Docility, tractability are very common traits in domestic animals, and make it possible to herd them and confine them within relatively simple fences.

In plants we see the same thing as in animals; the domestic plants differ from their wild relatives in some way that makes them more useful to mankind, and at the same time dependent upon his care. One need only point out a few examples of this, the high yield and tough axis of wheat, the increased fibre-production and non-dehiscent capsule in flax, etc.

The animals and plants, and the human race breeding them, belong together in one symbiosis-group, adapted to the country and climatic conditions. It would not be possible to exchange members of one group for those of another group without disturbing the equilibrium.

The Hopis and Zunis of Arizona in the desert have one domestic animal and they have a special kind of maize, and both are specially adapted to life in the desert. The maize can be planted at a great depth in hills containing a number of plants, with considerable distances between hills. The sheep are very small and hardy, adapted to desert conditions by their extremely small size. One sheep weighing a hundred pounds has only one head and one set of legs; two sheep, weighing a hundred pounds together, have two heads and two sets of legs, so that they can be in two different places to hunt the scanty herbs, and for this reason in conditions where the sheep of fifty pounds can just live, a hundred-pound sheep must necessarily starve.

It would not help the Hopis if "good" breeding-stock of bigger size were sent to Arizona and New Mexico to "improve" the local Indian sheep. Those three organisms, the sheep, the

drought-resistant maize and the Indian agriculturists belong together in their symbiosis-group in the desert.

It is very necessary to remember that domestic animals and cultivated plants must be adapted to the special climate and the special condition under which they are to be utilized. Great mistakes have been made when some arbitrary measure of value has been adopted to judge the value of animal or plant species. In animal breeding, the system of exhibiting livestock at agricultural shows, away from any means of judging their adaptability to special conditions of use, has done quite a lot of harm.

A very good example is that of the large Swiss goats in Holland and Germany. Both in Holland and in Germany practically all the goats are kept by very small farmers and labourers. The goats are small and they give very little milk, but they have the advantage of requiring only the coarsest feed—potato peelings, coarse hay cut along the roads, etc. The young females are bred the first autumn. Both in Holland and in some parts of Germany Swiss goats from the Saanen and Toggenburg districts were imported. Those goats give six and more quarts of milk daily, but they require the best of care, excellent hay and grain, and very good pasture in summer. Goats of this kind were used extensively to "ameliorate" the native labourers' goats. Very soon it was noticed that many people could not afford to keep those goats, especially as the females had to be kept for almost two years before they produced any milk; and as the goats were kept by the very poorest people, who could not afford to spend any money on feed for the goat, the result was a complete failure of the experiment. In one set of two villages in Germany the grading to Swiss goats was tried in village "D", whereas in village "R" no attempt at "improvement" was tried. The result was that, whereas in village "R" all the small labourers kept goats, in village "D" only the innkeeper, the preacher and the teacher kept goats, and the labourers and farmers had given them up as impossible.

When judged at a goat-show the large, well-shaped Swiss animals appeared to be vastly superior to the small labourers' goats, but in reality the small goats were vastly superior for the special purpose for which they were kept.

It is very difficult sometimes rightly to appraise the value of a breed of domestic animals. At first sight a breed of poultry, in

which the hens lay 200 eggs yearly, is vastly superior to a breed in which the hens lay 50, and yet the cheapest eggs are probably produced by such hens as the native poultry in China and Java, where everybody keeps only a few hens, and nobody ever thinks of giving them any food at all!

At the other end of the scale we see breeds that are adapted to very high levels of nutrition, such as the black-and-white Holstein-Friesian cattle. Such animals are adapted to countries where the pasture is of a very superior quality, and where plenty of rich hay and good beets and feed-grain are produced. In such provinces those cattle are vastly superior to such animals as the Kerry or the Normandy breeds, which are adapted to small, rather poor farms.

When farming conditions are improved, when by the use of artificial manures, the pastures produce better grass and more of it, and when all sorts of good feeding-stuffs are produced cheaply, it may become necessary to change from one breed of cattle to the other. We have seen this happen in the extreme east of Holland, where wet marshy heather was drained and manured and transformed into such good pasture that the local breed of small red-and-white cattle could be changed into the Friesian breed by repeated back-crossings.

(See Notes at end of Chapter Ten)

Chapter Ten

Improved Breeds and Local Breeds

When a geneticist, interested in applied genetics, travels, he finds that wherever he goes, in every species of domestic animals or cultivated plants, a distinction can be made between breeds to the selection of which much attention is given, and other breeds that just happen to exist without any special attention.

It happens that I have travelled somewhat, and have always made a point of trying to find out something about native breeds of animals and plants in the countries in which I have lived. I have come to the conclusion that the prevalent idea, that the highly-bred, pedigree breeds are generally superior to the unselected native breeds, is wrong. A superficial examination of the qualities of the different breeds generally shows the striking superiority of the highly-bred strains: but the more we look into the subject the more the picture changes.

One of the chief difficulties always lies in the circumstance that our standard of what constitutes superiority in a domestic animal is very often warped by the influence of the animal shows. When we compare the Javanese cow with a European large cow of the same age, basing our comparison exclusively on the obvious qualities of the two individuals before us, we must pronounce the European cow superior. When we put one of the miniature scraggy Hopi Indian sheep side by side with a Lincoln, there is no doubt about the fact that the Lincoln is worth more money. A Shire horse is certainly worth more than a Welsh or a Shetland pony, and it is excusable if from this fact we deem the Shire superior as a horse.

This way of comparing different breeds of animals or plants, however, is very superficial. We should never forget that in

deciding which of two breeds of animals is the better one, we must ask the question, for what circumstances the breed is required. We should not compare one individual of one breed with one individual of a second breed; the measure of superiority in a breed of animals is the way in which it fits the circumstances in which it must live. We can also say that that breed is superior which fits best into a certain symbiosis-group, or in a given system of agriculture considered as a whole. Or we may say that that breed is superior when, considered as a breed, it produces the maximum monetary gain for its owners in given circumstances.

One of the differences between breeds which strike us first is size. It is evident that when we compare a small animal with a large one, the large individual is worth more money. A large horse can do more work than a small one; there is more to eat in a large ox than in a small one. Clearly, however, this is a very shallow way of measuring superiority. If we have a farm of a certain size, this farm can carry more small sheep than large ones. It is clear that the annual production of mutton from that farm may be the same, measured in tons, whether a great many small ones are raised or somewhat fewer large ones.

Why is it that animal breeders are more apt to think size in individual animals is valuable in itself than plant breeders are to think the production per individual plants counts? If we look into this question, we remember that some time ago plant breeders made the same mistake. For many years quality in seed-maize was thought to be correlated with size and shape of ears. At special corn-shows, prizes were given for beautifully-formed, well-filled, large ears of maize. Most of us have almost forgotten that there has been a time when farmers believed large ears of maize were better than small ones, and that enormous size in mangolds was thought to be a sign of superiority.

Every plant breeder and every farmer now knows that in agricultural plants the quality to look for is yield per acre, not yield per plant. In buying sugar, a pound of small lumps is considered just as good a purchase as a pound of large lumps at the same price, even if one large lump is worth more than one small piece.

With animals the difficulty is that at the shows one animal is compared with one other animal, with the rare exceptions of

ton-litters of pigs or carloads of steers at some American shows. Obviously an imposing animal looks ever so much better at a show than a small one. In judging domestic animals, one should never compare one cow with one cow; what one should compare is two lots of cows that both fit a five-acre pasture. If a certain farm is just large enough to support ten cows of a small breed, it is obvious that although those ten cows are worth less in the market than ten much larger cows, ten of those large cows would be too much for the farm, and for this reason the yield of the ten small cows should be compared with that of six or seven of the large ones.

In certain circumstances size is very important, namely, where animals are for use on very poor pasture. This is clearly illustrated by sheep on the moors or in the desert. The heather sheep of Western Europe are very small. When we consider two of those animals, each weighing fifty pounds, those two animals, like the sheep of the Hopis, have two sets of legs and a head each; they can be in two spots at the same time to gather the scanty edible herbs. If we put a sheep weighing a hundred pounds in a herd of Heidschnucken, this animal needs approximately as much food as the two fifty-pound ones together; but as it has only one set of legs and one head, it can only be in one spot at a time. For this reason, if the pasture is just good enough to keep the small sheep, the large one starves. In the desert in New Mexico I have seen herds of small sheep grazing in spots that looked as if they would not support a grasshopper. In such circumstances, small size is an important quality.

Where conditions of agriculture are very favourable, a quick turnover is important. Rapid maturity is very desirable in animals that are kept at a high level of agriculture; but this does not mean that rapid maturity in itself is desirable in all circumstances.

Some domestic animals have to live in countries where the food is abundant at certain seasons, and scanty at others. Under such conditions rapidly-maturing horses or cattle are at a great disadvantage, for when the period of starvation arrives, young animals of such breeds are stunted. Their skeleton matures, and, when another period of plenty arrives, they can never pick up again, but become short and stunted, and remain so. This is illustrated by young cattle of excellent strains that have to grow up in such countries as East Africa. It is almost unbelievable

that such beasts are closely related to the beautiful cattle of Holland and Northern Germany.

Now the native cattle in such countries as South Africa, Java and parts of Bengal, are very slow in maturing. This means that a period of comparative starvation stops their growth, but not permanently. At the next season of plenty such animals go on growing where they have left off. On non-irrigated pasture the red Afrikaander cattle grow up slowly into beautifully-shaped large animals, while European cattle under similar conditions of pasture grow up stunted and miserable-looking.

The native Javanese cattle are extremely slow in maturing. Most of the cows produce their first calf at an age of seven years. On the other hand, such cows, when once they are full-grown, have never had any food but what they have been able to pick up for themselves in this over-populated country, on the little dykes between paddyfields, in the woods, along the roads. Such cattle are not worth very much money as individuals, but whatever they are worth is clean gain—they have never cost their owner a penny. The circumstance that this breed of cattle exists in Java makes it possible for the very poor small farmer to get his fields ploughed on time, and he even has a calf to sell once in a while.

This is animal husbandry at a very low level, but this level is the one to which the animal breeds must adapt themselves. When I worked in Java there was quite a lot of propaganda on behalf of a larger, quicker-maturing British-Indian breed such as Ongole and Hissar. It was proved very rapidly that those animals could not live in the conditions under which the pure Javanese cattle could exist in the densely-populated districts. As a remedy it was urged that the natives should plant food grasses on their fields instead of the usual second crops (maize, soyabeans, peanuts) grown between rice crops, and the experiment stations and private European breeders showed that, with this aid, such cattle could very well be raised. Some of the more enthusiastic people overlooked that the culture of grass on fields where cash crops are usually raised is economically impossible for the small farmers living a hand-to-mouth existence at the best of times.

If we apply any of the intelligent standards of excellence, in comparing the Javanese cattle with Holstein-Friesian or Hissar cattle, for Javanese conditions in the kampoongs, the larger

animals, far from being superior (as they look when judged as individuals), are so inferior to Javanese that advocating their adoption by the Javanese orang tana is folly.

The native chickens in Java only produce very few small eggs. For this reason European colonists have imported Leghorns, Rhode Island Reds and similar "superior" breeds. When comparing those European breeds with native kampoong chickens, however, we must take into account the fact that the native chickens are very well adapted to the conditions under which they live. Every householder has a few hens, and no money whatever is spent on food. The eggs are few, but the price they bring is all profit. The European breeds, kept in enclosures in large numbers, lay larger eggs, and when the owners of those hens can find a market at a remunerative price for those larger eggs, it may be profitable to keep them. It should, however, be remembered that in the conditions under which the natives keep poultry, the European hens are really inferior to the active, disease-resistant native ones.

Especially in places where a native population and a few Europeans live together, the qualities of the native breeds of domestic animals should be carefully studied from the point of view of economic usefulness to their owners before we decide to "improve" them by crossing with our imported European breeds. This is especially true when those European breeds are much better from the standpoint of their European owners. Milk production is of secondary value to hardiness and adaptation to unfavourable conditions in such native cattle as the Javanese. In favourable localities, such as on the mountain plateaux, it may pay Europeans to raise milk cattle, but this may never lead to the "improvement" of native cattle by cross breeding when the animals are intended for use by the natives, who cannot afford to have pasture for their animals.

Very often travellers have remarked upon the poor quality of native domestic animals, and it has been often said that lack of care, in-breeding, or "degeneration" were responsible for the unprepossessing character of such livestock. Very few people seem to realize that the qualities of such animals, which have been bred for untold generations in one set of conditions, are due to adaptation to often very special and sometimes unfavourable circumstances. Whereas it is easy enough to compare two animals of different breeds at an agricultural show, and to

see that one is larger or fatter than the other, it requires far more intelligence to find the specially-valuable qualities of the mean-looking breed when compared with the good-looking one.

In most parts of France every farm has a small colony of nondescript grey rabbits in hutches. From the point of view of a rabbit fancier those animals are not worth much compared with the beautiful rabbits seen at the shows. When, however, we live for some time in a French village, we begin to appreciate the quality of those farm rabbits. The hutches are capacious brick or stone affairs, and every day a lot of green stuff, weeds, grass, maize stover, etc., is dumped in for the rabbits to pick over. No money is spent on grain, hardly any sickness is ever seen. On Fridays, when the rabbit-skin dealer comes around, one or two rabbits are killed by him and prepared for the Sunday dinner, and when all is said and done, this is a very economical way of obtaining such a fine dish when one is as much afraid as a small French farmer to spend money.

When we take the trouble to look for it, we often find very remarkable qualities in non-pedigree domestic animals. In ducks we have two native land-races in Holland, the flying ducks around the town of Akkrum in Friesland and the small black ducks of the county of North Holland. Around Akkrum the ducks are owned by the town. Every farmer by paying fourpence a year per nest can get the right to place globular straw nesting-baskets with a narrow entrance neck high up in the trees around his house, and to gather the eggs laid in them. The farmers do not feed the ducks who fly out to the marshes to feed. Such duck eggs are cheaply produced!

The small, black, white-breasted ducks around Edam and Purmerend are caged up during the day and let out when it is dark. They forage in the pastures and along the sides of the canals, and come home very early in the morning to lay their eggs during the daytime. When white and spotted Indian Runner ducks were tried by the duck farmers, the peculiar virtue of the small black ducks became very apparent. As the ducks damage the sides of the watercourses, many complaints reach their owners when they are seen abroad in daylight. In this respect the discreet small black ducks who did their work during the dark hours and were home during the day were very superior!

In Java, the home of the Indian Runner ducks, these ducks

were hatched under Muscovies or artificially in marshy spots around the south coast. Specialists used to buy up the ducklings at an age of four to six weeks and start herding them. One could meet large herds of ducks being driven slowly along the road, mostly during the night, by a man with a small flag on a long handle. When a suitable spot was found, such as a recently-harvested paddyfield, the ducks were allowed to forage and bathe. When they wanted to rest, the man put a lattice fence around the troop and curled himself up to have his siesta. When the ducks started to lay he sold the eggs in the villages he passed. Finally, after some months he delivered those of his flocks he had not sold by the way to one of the large markets and returned home by train. (Things have probably changed since 1939.)

People obliged to exist at a low standard of living generally own animals that are beautifully adapted to their needs. I am convinced that it would pay to utilize the economic qualities of some of the Chinese domestic animals. I have seen a Chinaman bring a couple of baskets with the common small buff chickens one sees in southern China to the quay where a ship was being loaded with grain, let them out of the baskets to forage all day and take them home again at night.

When we want to compare domestic animals, adapted to a low level of agriculture, with highly-bred pedigree stock we must always remember that very different qualities are wanted in domestic animals that are kept intensively and have to show a quick return for expended energy, care and food from what we want in animals kept extensively, a few to every owner. In the latter category of stock the animals are able to find all their food themselves, because each animal can exploit its own area free from competition. Where animals and birds are kept intensively, they are kept massed together, so that the little food that usually goes to waste is of comparatively very small importance. Food must be brought to such animals or good pasture must be provided.

Just as a group of domestic animals will gradually become adapted to a low level of agriculture, in conditions where a high level of care and food are present the domestic stock gradually adapts itself to those better conditions. The great productive black-and-white cows of the fat polders in Holland are adapted to this sort of pasture. Here selection of the most productive families has improved the breed.

When conditions of agriculture arc improved, when artificial manures make possible better crops of grass and hay, a corresponding change in the quality of the livestock used is necessary. When we find a poor breed living under poor conditions, we must carefully determine whether this breed is good enough when we change the conditions. Often this would not be true. Then it is advisable to try a breed adapted to better conditions, and if it fits, to change over the local breed by repeated cross-breeding. We have seen examples of this in sandy and marshy parts of Holland where by drainage and manuring the quality of the pastures was greatly improved. In such parts of the country it paid to change over from the old, small breed of cattle, adapted to local conditions, to larger and more productive animals.

It is very easy to make the mistake of confusing the raising of the general level of agriculture and a corresponding adoption of breeds of animals fitting into such conditions, for the effect of selection in improving the quality of the animals in the country.

In a country like Holland the general size and production of the cattle one meets at the market nowadays has certainly improved very much over what they were thirty years ago. It would, however, be erroneous to think that this improvement is a triumph of the animal-breeder's art. Excellent productive cattle, adapted to very good pasture, were present in the country a hundred years ago in definitely favourable spots. What has happened is mainly an improvement of the level at which agriculture exists. With the growing industrialization of the country and the enormous growth of the population it has become worth while to buy great quantities of artificial fertilizer to improve the pastures and extend the area where the very productive breeds of cattle were kept. The former breeds, adapted to low levels of feeding, have not been improved—they have been supplanted.

This is all very nice as far as it goes—but we must never lose sight of the fact that while the area to which highly productive cattle are adapted has been greatly extended, there is always left a certain area where agriculture is still at a low level. When we make the mistake of thinking the cattle have been improved in quality all around, it is easy to make the corresponding mistake of thinking that a further improvement will result if we force all the farmers to use bulls of the better, productive breed.

A long time ago this mistake was made in Holland, in the county of Gelderland. When it was evident that the general quality of the cattle was improving at the same rate at which agriculture as a whole was progressing, a regulation was passed prohibiting the use for breeding of unlicensed bulls. The result has been that the men responsible for the judging have chosen the type of the productive Maas Ryn Ysel and Black-and-White Holland breeds as their ideal. This has led to a rapid improvement (from a showpoint) of the cattle in the richer districts. In this county, however, there existed a special breed of small scrubby-looking cattle, adapted to the small crofters' farms in the poorer sandy districts. By obliging those farmers to use bulls of the so-called "better" (but under the circumstances really inferior) type, many small farms, where formerly one or two cows were kept, have been driven to give up keeping cattle at all. I have spoken to many of such small crofters who now keep a few goats in what used to be the cow-barn, because the sort of stock they were breeding from the approved bulls were getting "too large for their farms".

Such mistakes must always be made where false standards of quality are used. I repeat, *there is only one real measure of superiority in domestic animals, i.e. adaptation to the conditions of agriculture into which the breed must fit.*

It is a great mistake to look down upon local "unimproved" breeds of domestic animals and plants just because each individual compares unfavourably with a corresponding individual of an "improved" breed.

We should never compare individuals with individuals, but always breeds with breeds. The best breed of pig or cow is the breed that best enables a farmer to make his farm pay.

When travelling through the Ozarks in Arkansas I came to villages where a few half-breed Indians and Hillbillies farmed the forest. An enclosure was fenced for corn, and in spring the razorback swine were turned into this enclosure to root out the stover, grub out most of the worms, and turn up the earth to the point where just a few finishing touches were necessary to get the soil ready for ploughing. After the corn was up, the women and children actually had to do some heavy work hoeing, but after the crop was harvested the pigs again did their share. Those razorback pigs were not fed, they "found themselves". So did the few miserable-looking scrub

cows wandering in the forest. Those cows bred, and by the simple expedient of muzzling the calf part of the time, each cow could be made to yield one or two quarts of milk for the family. This was agriculture at its lowest ebb, but both the hogs and the cattle were beautifully adapted to this level, and to the minimum amount of energy hookworm, malaria and moonshine left their owners. Were these animals inferior in the circumstances?

Get rid of some of the chronic human diseases and some of the illiteracy in such a district and everything changes. A farmer with some energy and pride can make a success of agriculture at a higher level, and to do this he needs a different type of hog and of cow: but to improve the cattle and the hogs by crossing with Shorthorn or Yorkshire will not be the right way to set about changing the state of things intelligently.

As local unimproved breeds of animals are generally looking their worst at the shows, it is very easy to rate them much worse than they really are. When we look for them, most of such breeds have their very good points, points we could very well do with in some of the "superior" breeds.

Very often the excellent quality of a local breed can be made use of in a system of agriculture at a much higher level than the one into which the pure breed fits. Two qualities are common in such stock—fertility and cheapness. In Germany the red Bavarian sows are famous for the way they fit into a scheme of raising first-generation store pigs when bred to Large White Yorkshire boars. Native sheep of different breeds are excellent to use for breeding first-generation lambs from Karakul rams for the fur trade. The Javanese cows, when bred to Hissar or Madura bulls, produce excellent, active, quick-moving and long-lived bull hybrids for heavy transportation work at the sugar factories.

In different respects, local unimproved domestic animals are worth studying. I have tried to warn against the superficial way of condemning them which is fostered by the habit of comparing individuals at the agricultural shows.

NOTES

I am discussing these two chapters together because they seem to me to deal with much the same subject. In them, Hagedoorn exposes one of the most

serious, yet most common, errors in the numerous well-meant and officially sponsored schemes of livestock "improvement".

The idea that the productivity of a breed is independent of husbandry is widespread yet false. Hagedoorn, being widely travelled, has drawn well-chosen examples of that fallacy from territories as distant as Java and Arizona. Yet similar examples can be selected from much nearer home. Premium sires and the schemes designed for their utilization have long been the darlings of our Government Departments responsible for livestock "improvement".

In Scotland there are, of course, wide distinctions between the natural fertility and productivity of different districts. The Lothians, for example, are fertile, the Western Isles relatively barren. As a natural and inevitable result of such variable fertility, the livestock of the Lothians are both bigger and more productive than the livestock of the Western Isles. Any traveller journeying from Lothian to the Western Isles would be struck with the apparent inferiority of the livestock of the latter region. It would be easy for him to assume that it would be a tremendous improvement in livestock production were livestock from the Lothians transported to the Western Isles to supplant the types of livestock native there. It is an error, however, and an error supported incidentally by certain assumptions implicit in genetic theory, that the Lothian livestock would retain their superiority in size and productivity under the husbandry conditions of the Western Isles.

Actually, unless it were both physically and economically possible first of all to raise the level of crop husbandry of the Western Isles to Lothian standards, the importation of Lothian livestock would be a waste both of time and money since its size and productivity would certainly sink to the lower level that the fertility and husbandry systems of the Western Isles were able to support. Hagedoorn emphasized this point in italics (p. 75) when he wrote:

"I repeat, there is only one real measure of superiority in domestic animals, i.e. adaptation to the conditions of agriculture into which the breed must fit."

Chapter Eleven

Aims in Animal Breeding in Relation to Agriculture

The most important point to decide in the breeding of any kind of animal is the ideal towards which we want to breed. The first thing we must know is just cxactly what we want, for without a definite goal we can never hope to produce a true-breeding group in which every animal shall be valuable.

In animals that are bred for show purposes only, such as many rabbits and pigeons, there is no real fixed ideal of quality, breeders of these animals being governed by fashion while the way in which fashion changes is determined by chance. The ideal in such animals is never to produce large numbers of individuals that will be all alike, but each breeder's aim is to produce a few animals that will win in the shows in competition with the animals produced by his fellow-fanciers.

When we are dealing with animals and birds that are bred for profit, the aims should be well defined and clear, not nebulous and dependent upon the fashion of the moment. In such a breed we aim to produce a group of animals that shall all be alike in this respect, that under suitable conditions they will produce a profit.

For different reasons it is very hard to bear in mind that in such breeds everything should be subservient to usefulncss. The first difficulty lies in the circumstance that when a group of animals becomes more and more pure for its inherited make-up, the animals that form the group will be more and more alike in all respects and have a set of recognizable external qualities—size, colour, conformation. As those qualities in a pure breed assume something akin to hallmarks, guaranteeing purity of breed, those qualities will become important out of all propor-

tion to their real value. As it is very much easier to judge such characters as type, or size, or colour than real value, there is always some danger of this happening. Especially is this true in animal groups in which real economic value can only be judged in one of the two sexes. In milk cattle and laying breeds of poultry the males are indispensable to make the females produce new females, but they do not themselves contribute to the economic value of the breed. As in those animals only a few males are required, it becomes necessary at every generation to decide which males to destroy and which ones to keep alive for breeding. It is clear that the breeder who is set this task of selecting a few males is very likely to compare the males at hand in regard to their personal qualities.

The shows have had very much influence, for if we bring milking breeds of cattle or egg-laying strains of hens to the shows, the only basis of comparison there can be are fancy points, and those points are apt to assume an importance out of all proportion to their value.

When a breed of animals is bred for profit, but at the same time it is also shown regularly, we have two independent sets of standards by which to judge the value of individuals—beauty (fancy points) and utility. In such a breed as is kept with those two different objects it will certainly often pay better to breed beautiful animals for sale, than to keep such animals for their real economic purpose. The most successful breeders of show Guernsey cattle or of show Hampshire Down sheep make more money than dairymen or sheep-farmers.

It can easily be seen, however, that it is very much more important for farming as a whole that cattle and sheep shall be profitable as farm animals than that a few prominent breeders shall make money by showing.

In poultry breeding it has been possible to separate breeding for the shows from breeding for profitable egg production, so that in many breeds we now have utility strains which are never shown and which are valued according to economic usefulness, and show strains which are judged at the shows and in which economic production is unimportant. In breeding sheep it would probably be impossible to keep special show strains that would be bred only to compete at the shows—it would be too expensive a hobby; the "sheep fancy" can exist only because farmers are led to believe that there exists a connexion between

show type and practical value, so that the show breeders find a ready sale for their young rams at profitable prices.

The question must be faced is there any correlation between the qualities desired at the shows and real economic value?

One of the shrewdest and most sensible statements on the subject in hand was made by Boutflour a few years ago. His argument was that either there is a correlation between show points and utility or there is not. If there is such a correlation, breeding for economic value will automatically give us the right type and it will be unnecessary to give special attention to those points. If, however, there is no such correlation, breeding for those show points will surely handicap us in our attempts to improve the breed from an economic standpoint.

A very prevalent idea seems to be that a selection for certain externally visible qualities is necessary in order to produce animals of good "constitution". The idea seems to exist in certain circles that by selecting only for yield it would be possible to produce a strain of cows to yield 2,000 gallons a year regularly, but in which the animals themselves would be miserable beasts with a very poor constitution, or in poultry to get 300 eggs but have no hens left worth talking about! It is hard to find the origin of this ridiculous idea. Surely it might be said that the 2,000-gallon cows or the 300-egg hens, if they could produce this enormous value by means of an economically balanced food consumption, would have just exactly the constitution the farmers wanted in their animals. Of course we want to have the right constitution in our animals, but when we set about to measure constitution, the only test we can apply is the ability to produce a lot of milk (or eggs) at a low cost, and to keep up this production during a long lifetime.

Both in milking Shorthorns and in the Black-and-White Dutch cattle, the average useful life (milk-producing period) of a cow in the herds of the pedigree breeders is about two years. At first sight this would show those pedigree cows to be of very poor constitution, but in reality there is no reason to believe that there is any essential difference between those pedigree cows and the rest of their breed. It only means that the necessity in those herds of paying sufficient attention to show points greatly interferes with the selection of really profitable cattle.

We must realize that in such breeds as the popular breeds of milk cattle two sets of ideals exist. The users aim to get animals

that will be a good investment, and there are two sources of income from cattle, the milk and the carcasses of the superfluous bull calves and of the milk cows themselves when they are no longer profitable.

The relative value of milk and meat in a breed of cattle depends upon a great many different things. Where population is very dense, and where milk is expensive, the profit from milk is very much more important than that from meat. Milk production, however, can only be profitable when there is a good market for the milk, when sufficient labour is available, when there is a continuous supply of food, and lastly when cows are kept that will turn this food into milk economically. In countries where markets are far away, where labour is scarce, expensive or unreliable, where good seasons alternate with periods of drought, conditions are better for beef than for milk, provided the sort of cattle kept is adapted to the special conditions—cattle that turn grass into beef rapidly and profitably.

It has never been conclusively proved that the inherited make-up that produces a profitable milker will prevent that same cow from being a profitable meat-producer. Let us suppose that, physiologically, it is possible for the animals in one pure breed to produce milk profitably in one set of conditions, and to produce meat economically in another set of conditions. If this would be physiologically possible, would it be really worth while to aim at the creation of a real dual-purpose breed?

When answering this question we must remember that a real dual-purpose breed of cattle, in which the cows would produce plenty of cheap milk and would fatten rapidly and economically after ten years of milk-production, would perhaps have only a very limited range of distribution, and that only in a very few countries would conditions be such that a breed like this would be more profitable than either a specialized milk breed or a specialized beef breed. For reasons I will explain later I will leave the quality of the superfluous calves out of consideration here.

How would we set about to produce a real dual-purpose breed of cattle? When we think of the enormous difficulties in evaluating the qualities of the breeding stock, we must realize that the problem would be extremely difficult. In selecting a bull of such a breed we would have to know that his daughters

averaged very high in profitable milk yield, but that those same daughters at ten years of age were still worth fattening!

How about the present so-called dual-purpose breeds? A few breeds are kept for which the promoters claim that they are valuable both as beef cattle and as dairy cattle. The milking Shorthorn and the Black and White cow in the south-western part of Holland and in north-western Germany are breeds for which this is claimed. So is the Redpoll.

Such dual-purpose cattle are produced by crossing a milking breed with a beef breed. In Holland the Friesian breed used to be bred as a dairy breed, until for show purposes English Shorthorn bulls were imported and employed. In England the milking Shorthorns were produced from the same crosses. The two breeds look different because in England the object was an improvement of the Shorthorn in regard to milk, and in Holland the object was improvement of the local dairy cows mainly for show purposes. Both in England and in Holland only part of the original breed was changed: in England the milking Shorthorn exists by the side of a pure beef-Shorthorn, while in Holland in some parts of the country the original dairy breed is still being kept and selected as such.

In both dual-purpose breeds we see exactly the same thing. Within the breed we find extremely good dairy cows, and within the breed we also find excellent beef animals—but animals that combine both qualities are very rare. It is true that in both countries are exhibited cows that show the beautiful straight back and well-filled flanks of ideal beef animals, and that also produce a very large amount of milk—but such cows are in the nature of freaks, are far from typical, and certainly do not tend to reproduce their kind.

Wherever there has been a tendency to pay sufficient attention to milk yield in such cattle, the bulls have always been judged at the shows as if they were bulls of a beef breed. This has been possible because up to not so long ago it was sufficient for a bull to produce a dozen excellent milking daughters to be considered a valuable bull in regard to milking quality, no matter how many of his daughters were mediocre or poor milkers. Nowadays, when we are hunting for bulls that have shown themselves to be capable of producing daughters of high average quality and at the same time sons that look like beef bulls, such bulls prove to be extremely rare. The fact that in

the Dutch Black-and-White breed it is so very much easier to find bulls of proven breeding value, as far as milk is concerned, in America than in Holland does not prove that such bulls are not equally plentiful in Holland. They exist in Holland just as well as in the States, but if we limit our search to those bulls only which are of monumental beef-appearance, we necessarily find only a very few proven milk-sires in that limited group.

Boutflour has repeatedly pointed out that the circumstance that we find very much more variation in regard to milk in the so-called dual-purpose breeds than in the specialized dairy breeds, and that we find exactly the same difference between the variation in beef-quality in a dual-purpose breed compared with a real beef breed, shows that selection for beef only, or milk only, is much easier than selection for two ideals in one single breed.

Both in England among the Dairy-Shorthorn enthusiasts and in Holland among the fanciers of our Black-and-White and of our White-faced cattle, the selection for beefiness in bulls is defended with the reasoning that good quality from a butcher's standpoint is of very great value. It is certainly true that our Dutch Black-and-White bull calves and our old Black-and-White cows, compared head for head with Jerseys of similar age, are worth more money; but the whole thing is not as simple as this!

Probably the average age at which a cow in a dual-purpose breed is butchered is four to five years. Such a cow is worth quite a good sum of money; but it would be much more profitable for farmers in general if the cattle were of such a quality that the cows could be profitably milked up to an average age of ten years. In a cow that has produced 2,000 gallons of milk yearly for eight years, the butchering value of her carcass is negligible compared with the value of her milk. Even the value of a very good steer is not much compared with the profit such a cow has produced.

In parts of the world where milk is very valuable, it pays to milk the cows and sell the calves. I have seen it stated very often that in a dual-purpose breed the butchering value of the calves is so much greater than that of dairy-calves that this alone would make a dual-purpose breed profitable. I do not know how this would be in a real true-breeding dual-purpose breed, for I do not happen to know such breeds. In a milking breed

however, it is not necessary with good management to raise surplus "dairy" calves from the dairy cows which are not destined to reproduce their breed. I know that such cows, when mated to a Hereford or Aberdeen-Angus bull, will produce calves of excellent butchering value.

In considering the difficult question of dual-purpose standards in all animals, such as meat and wool in sheep, work and beef or work and milk in cattle, we must remember that the idea that selection in one direction must surely produce degeneration in a second direction is not necessarily true. It tends to be true in breeds in which the variation has been recently heightened by a cross; and for this reason it is certainly true that selection for milk in a dual-purpose breed, which has been produced by cross-breeding less than a century ago, tends to make the breed less valuable from a butcher's standpoint and vice versa. In reasonably pure breeds, however, it might be possible to attain some progress in one direction while holding on to some important other quality for which the breed is pure. Again, when considering two different qualities in one breed it is always necessary to remember their relative importance.

In Germany and Switzerland it has been found that letting the cows do light labour has no bad effect upon their milk yield; on the contrary, where cows are never let out in the sunshine light work at hay-time actually improves both yield and health. In such instances it would be the height of folly to pay so much attention to such qualities as speed and intelligence, that bulls which produced specially quick-walking daughters would be patronized rather than bulls with good milking daughters!

In animal breeding it seems to be very much more difficult than in plant breeding always to remember that our aim must be profit to the farmer. I know many more cases in animal breeding where standards towards which the breeders aim deviate from the most profitable relation between incoming and outgoing than in plant breeding. At first sight this seems surprising, because in both instances the farmers must try to make a living—by raising either animals or plants. The only explanation that I can find lies in the circumstance that the farmers who have to use the animals have not sufficient voice in the setting up of aims towards which their animals are bred. We must always remember that our agricultural animals are highly polygamous. A relatively small group of breeders can, by pro-

ducing males, have a very great influence upon the trend of things in animal breeding. We cannot reproach our prominent breeders, organized in herd-book societies, that they arrange things as looks best and most profitable to themselves, as they have their living to make as well as the ordinary farmers. These breeders are the ones who take an enormous interest in the shows, and it would be very surprising indeed if, with any class of agricultural animal, competition in the shows were to push things in the direction of making the animals selected more profitable for ordinary farmers to breed.

The farmers themselves, the real users of the animals, do not tend to raise their voices. When they become prominent in any way, they tend to enter the ranks of the pedigree breeders!

Whereas in matters of plant breeding I have always, as a consulting geneticist, found it sufficient to help the breeders attain the aims they set themselves, in animal breeding I have often found it necessary to help the breeders to establish standards of quality that would tend to make the animals fit more economically into existing schemes of agriculture.

NOTES

A chapter full of ripe experience and packed with common sense. There is not a sentence in it with which I disagree. The division both in interests and in aim between the stud-breeder and the commercial farmer—a division which tends to bedevil so much of our animal husbandry to-day—is exposed with laudable clarity and, incidentally, without the introduction of a single genetical term!

Hagedoorn had a profound knowledge of humanity as well as of animal breeding. He wastes no energy on attacking the pretensions of the pedigree breeders. Certain other geneticists might do well to follow his example. The stud-breeder is not and cannot well be expected to be a disinterested enthusiast for livestock improvement although for purposes of advertisement and propaganda he may claim to be so. As Hagedoorn wisely wrote:

"We cannot reproach our prominent breeders, organized in herd-book societies, that they arrange things as looks best and most profitable to themselves, as they have their living to make as well as the ordinary farmers."

Chapter Twelve

Importation

When conditions of agriculture change it will very often be necessary to change the breeds of domestic animals and the kinds of cultivated plants accordingly. Sometimes existing breeds are sufficiently variable to permit of a change in the average quality of the animals in a breed, but a sufficient amount of variability does not necessarily always exist. In such circumstances two ways are open: we can ameliorate an existing breed by cross-breeding, or we can look in a foreign country for a pure breed that just fits our requirements.

The importation of a ready-made breed from a foreign country has seldom been tried systematically; yet it is obvious that it would be illogical to go to all the trouble of improving an existing breed by means of cross-breeding when another breed could be imported ready made. The importing of foreign breeds can be very profitable for people who take the initiative—but we must always be able to distinguish between this kind of profit and the real merit of the imported breed.

The first men to keep a newly-imported breed of animals are very likely to make money out of their work, for while a breed is new its very rarity and novelty produces a demand that is for a long time ahead of the supply of young breeding stock. This high demand, however, does not necessarily prove the value of the breed.

The importation and testing out of new, foreign breeds should really be in the hands of the Governments, for on the one hand it is illogical that the individual breeders should take this risk, and on the other hand it is highly undesirable that an indifferent or even a worthless importation should be propagated just because the first breeders earn their money that way.

One curious aspect of the importation of a foreign breed is the fact that the variability of an imported group is always only a fraction of the original variability of the breed in the country of origin. This is partly due to the circumstance that a selected group is collected for the importation, but partly also to the fact that rare genes present in a few members of the breed are very unlikely to be present in the small group of imported animals.

Dogs are more often imported into foreign countries than any other animals, and they illustrate my point very well. The Samoyede in its original country is bred in all sorts of colours; in England the dogs imported were all white. The Newfoundland dog at home is very variable, all sorts of ears are seen, and different types of coat in many colours. In England we know the dog as a very little variable breed, in which all specimens have one kind of ears, one sort of coat, one way of wearing the tail.

When somebody notices an excellent breed of animals in a foreign country, he may be so enthusiastic that he starts to import the breed into his own country; but very rarely is the simple precaution taken of first trying out the quality of the animals of the new breed, when born and raised in the new country.

The failure to observe this safe rule can result sometimes in very striking disappointments. A few examples will suffice.

When it was deemed advisable to improve the size of the native Javanese and Sandalwood ponies in the Dutch Indies, the veterinary officials who were responsible for animal breeding in Java hit upon a scheme of importing hunter mares from Australia. It was thought that the great size of those mares would be a valuable quality to impart to the small native ponies. Nobody thought of the necessity of observing just how big those Australian hunters would grow when they were born and raised in Java. The authorities did not realize that the quality (here size) of those imported individuals was only partly due to their genotype, but partly also to the conditions under which the animals grew up; they forgot that only the genes from those mares would be transmitted to their offspring, and not the result of their upbringing.

By chance I happened to hear that at the stallion depot at Padalaran two Australian hunter mares had been imported

pregnant from hunter stallions, and that the hunter foals had been raised at the station with every care that could be given to those valuable animals. When I went there to look at the animals they were over two years old. What was my surprise when I saw them being exercised in a long string of Sandalwoods, and that they were not a bit bigger than any of those ponies.

A very similar case is that of the Dutch-Friesian cattle in East Africa. When animals of this breed were first imported into German East Africa, as it then was, the idea was to improve the size and general quality of the native cattle. It was soon found, however, that whereas the adult animals imported from Europe retained their size and general qualities, the young born in the new country never grew up to a good size. They always remained short and dry and very much undersized. Calves imported into this country at an early age also showed the same general lack of quality. The fact that this breed was not adapted to climatic conditions in tropical Africa was overlooked.

Exactly the same mistake was made in Java when Ongole cattle were imported to improve the Javanese cows. The precaution of first discovering how pure-bred Ongole calves would grow up under Javanese conditions was neglected.

The case of the Saanen goats in Holland and Germany has been treated of elsewhere. This was another example of the importation of a breed that was excellent in its own country, but totally unsuited to the conditions of agriculture in the new one.

It should be remembered that the importation of foreign breeds into any country may be extremely valuable, and from an economic standpoint very much better than trying to change an existing breed of animals to fit the changed conditions; but the very first thing that must be determined is whether the new breed, raised under local conditions, really fits those conditions. This is done in the cheapest way by the importation of a few very young animals of the breed to be tested, or by the importation of a few pregnant females.

When, as a result of such experiments, it is found that the imported breed is more valuable than the corresponding breed it is intended to replace, the question arises which is the cheapest way of getting the new breed established in place of the existing one.

When we are dealing with a rapidly-reproducing animal, such as a breed of poultry or a breed of pigs, it is evident that pure-breeding within the breed is the most profitable way of doing things. With cattle, however, or horses, reproduction is so very slow that it would take too long for multiplying the new breed to take effect. The best method in such circumstances is to breed the females of the old breed to males of the imported breed, and to repeat this process of cross-breeding with the cross-bred females and pure-bred males, and so on. The change of the horses in the Dutch provinces of Limburg and Zeeland by the Belgian breed in the last years of the first world war and in the first years after it is described elsewhere. It is surprising to see how few back-crosses are necessary to make the last traces of the original breed disappear.

Again, however, I wish to repeat my warning that we must never forget our preliminary precaution of testing out the new breed in its pure form in the agricultural conditions of the country into which we want to import it.

As the importers of a foreign breed are very likely to make a financial success of the importation, even when the quality of the breed is doubtful, the preliminary experiments should not be left entirely to private enterprise, but the Government of the country should assume the financial risk of this and see to it that the experiments are made in such a way that an unbiased opinion of the value of the imported breed can be formed.

When it is decided to import a foreign breed, it becomes necessary to choose a number of animals to buy. As a rule it will be found that the breed in its own country is rather variable. Which animals should we take? In the first place it would be unwise to buy exceptional animals. We must have tested the quality of the average representatives of the breed in their new surroundings, and we have to deal with average representatives of the breed. Exceptionally outstanding individuals are apt to disappoint in their breeding behaviour. In the second place it is better to buy young stock than highly-priced old animals, for obvious economic reasons. In the third place it sometimes pays to make a study of the colour inheritance in the breed to be imported, for it is important that the imported lot should be as uniform as possible in appearance. If we can choose between several colours, we can best choose a recessive one—but especially must we warn against choosing a colour that

belongs to the unfixable group. To take an example, if for any reason anyone should want to import Shorthorns into a new country, it would certainly be wise to eschew the roans and import only the reds and red-and-whites, for this would rid us of three colours once and for all. If anyone wanted to import the Dutch Belted cattle into England and had the choice between reds and blacks, he should take the reds, as they breed true to colour, which is important in a new breed.

In any event it is unwise to pay too much for exceptionally good animals. We can leave this until the time when we have, by repeated back-crosses, changed our local breed into the imported one. When we have progressed so far it will pay to add the finishing touches by importing something extra special—but not before. Finally, one should import few females but as many males as possible, in order to be able to make good progress in changing the breed.

Chapter Thirteen

The Production of First-Generation Hybrids

For certain purposes first-generation hybrids between distinct breeds may possess certain advantages over pure-bred animals. This is especially true where great uniformity is desirable, for it is a general rule that hybrid lots are more uniform than pure-bred lots of animals.

In so far as heredity is the cause for variation, differences between animals of one group arise through the fact that some animals in the breed are impure for valuable genes, so that they impart these genes to only half of their offspring. If even a small proportion of heterozygous individuals are present in the breed, two heterozygotes will occasionally mate, and such matings will produce 25 per cent. of offspring in which the gene in question is lacking. It is rather a difficult job to eradicate this impurity in any breed, especially if one does not own sufficient animals to be independent of animals purchased from others. Now this is where cross-breeding produces uniformity. Let us suppose that in one breed there is some impurity for three genes, A, B and C, and that in another breed there is also some impurity, but for three different genes, D, E and F. This means that, as long as we breed those two distinct breeds separately, we will always have some recessive aberrant individuals lacking A or B or C cropping up in the one breed, and animals lacking D or E or F in the second one. What happens when we cross animals of the two different breeds together?

In our first breed may be produced germ-cells that are deficient in A or B or C, but all germ-cells will contain genes D, E and F. Reversely, the second breed may be impure for those last-named genes, but as the animals are all pure for A, B and C, those three genes are passed on to all the first-generation

hybrids. As a result the hybrids will all receive genes, A, B and C from one parent, and D, E and F from the other one. The hybrids will also receive all genes that are common property of both parental breeds. We can state it in the following way: the effects of the impurity of one breed in respect to certain genes are hidden by the circumstance that in each case those genes are present in all the germ-cells produced by the second breed.

This result of cross-breeding, the correction by one parent of the causes of variability due to the other parent, may be illustrated by a simple example. When we want to exclude the light from a window, we may possess only some old window-blinds with holes in them. When we stretch one shade over the window, the holes in the curtain will admit some light. When we substitute the other curtain, we see the light through holes in other spots. When, however, we hang one curtain on top of the other one, the holes are not very likely to correspond; in spots where the first curtain has a hole, the other curtain is tight, and where the holes come in this second curtain, they hang over spots in the first one, that do not permit the light to pass.

This is one of the chief reasons for the striking uniformity in lots of first-generation hybrids. Often, however, the hybrids are not only as good as the best members of the two breeds crossed, but decidedly better. The explanation of this fact is rather similar to the other one. In fixing the breeds, it is occasionally possible that important genes may be dropped from the stock altogether. In selecting a breed of poultry for size and shape of an enormous crest, it is possible that one or two important factors necessary for good fertility are lost. Possibly the same is true of a second breed in which we are selecting for enormous size or length of feather. Again, those weak spots in the heredity of such breeds are not very likely to correspond, and in so far as they do not, the hybrids between the breeds will inherit some of those factors from one parent and some from the other, so that they will have a full complement of them. When we cross two highly-bred exhibition breeds of poultry, let us say Polish and Brahma, the fertility of the resulting hybrids is often surprising.

In animal breeding infertile hybrids are sometimes bred between related species. The mule is a classical example. When we go to the markets in mule-breeding centres in summer, where the mule foals are coming to market following their dams, it is exceedingly remarkable to notice the mixed lot of mares of all

sorts of breeds and of no particular breed at all, and to see how all the foals resemble each other, as if they had been cast in one mould.

A similar case is that of the Muscovy duck hybrids that are produced in thousands in some parts of France by mating Muscovy drakes with ducks of all sorts of large breeds. The hybrids are bred for meat and especially for the production of pâté de foie gras. They are larger than either parent, they have the advantage that the ducks grow as large as the drakes and that they fatten readily at an early age.

The cross-bred geese that are produced in some parts of America for the Christmas trade by crossing Canada ganders with common geese come in this same category.

Sterile hybrids, produced for use, have one great advantage over fertile hybrids, namely, that the owners are not tempted to use them for breeding purposes. When hybrids are of exceptionally good quality, people may be tempted to use them for breeding purposes, often with disastrous results, as we will presently discuss.

Among cattle some combinations of breeds have an excellent reputation. An English example is that of the hybrids between white Shorthorn bulls and polled Angus cows. The hybrids happen to have a peculiar colour, caused by a combination of the roaning factor from the Shorthorn with black coat-colour, and this coat-colour serves as a trade-mark for the hybrid calves in the markets where they are sought after, because fatteners know their excellent quality for their purpose.

In Java, the hybrid bulls, bred from Ongole fathers and Javanese mothers, are much prized as carriage bulls, and in Madura first-generation hybrids between Balinese and native Madurese cattle are well known as being eminently suitable for the bull races which are so popular there.

Wherever the Arabian horse has penetrated it has been shown to produce excellent first-generation hybrids with several different breeds of horses. Even the ungainly Manchurian pony produces an excellent riding horse when mated with the Arab stallion. Some of the very best cow-ponies are produced by mating an Arab with the native mustangs.

In the goat some combinations of breeds such as the Anglo-Nubian and the Swiss-Nubian are noted for their excellent milking properties, and also for their longevity and resistance

to the common diseases. In one of the French provinces hybrids between goats and sheep are said to be regularly produced in large numbers, but it should be noted that some combinations of goat breeds and certain breeds of sheep will not produce embryos that are carried up to their normal term.

In the sheep we have many examples of well-known first-generation hybrids, of which the Karakul sheep is the best-known example. In Persia and Turkestan, Karakul rams are commonly used to cross with coarse black-woolled ewes to produce the lambs that give the lustrous skin known to the trade as Persian lamb. In England different combinations of breeds in sheep are well known, such as the Border-Leicester × Scotch Blackface and Border-Leicester by Cheviot, respectively producing the Greyface and the Scotch Half-bred, widely used for crossing with Down breeds for early lambs.

In many instances, such as those quoted, the good quality of the first-generation ewes as milk producers is utilized by a complicated system of breeding in which such cross-bred ewes are mated with a ram of a third breed to produce the early hothouse lamb that brings an especially good price.

The dogs furnish only a few examples of this class. The poodle-pointer is one of the best-known examples. Those hybrids seem to inherit the cleverness of the poodle, but lack its impossible coat of wool.

When the pelts of the European fitch fetched a good price it used to be very profitable to cross male fitches with female ferrets. The ferrets are very fertile and excellent mothers, and the hybrids, while requiring a somewhat more elaborate diet than pure-bred ferrets, are not as difficult to raise to maturity as fitch while their pelts bring as good a price as fur. There was a time when it was very much worth while to mate a polygamous Canadian silver fox with common red fox bitches, in order to produce cross-fox pups for fur purposes.

In the breeding of laboratory animals the easiest way to produce great quantities of healthy and thrifty mice and rats of good uniformity is to cross good in-bred strains.

For a long time it used to pay to produce hybrid ducks from Campbell drakes and White Indian ducks for laying purposes. Continued selection and in-breeding has improved the Khaki Campbell duck so much, that in the mammoth duck farms in Holland this breed has superseded the hybrids.

In poultry the production of hybrids between breeds for direct use is more common than in other livestock. For table purposes few breeds surpass the Indian Game × Sussex cross. The disadvantage of the cross lies in poor fertility of the Game males early in the season, and it will pay the breeders to produce a special breed of Indian Game of good fertility for this special purpose. An excellent cross for the same purpose is that between the North Holland Blue male and Barnevelder or Rhode Island Red females. It used to pay well in Holland to use the same pens of hens in spring for the production of pure-bred R.I.R. chicks and later in the season, when the males were exchanged for N.H.B. males, for producing chicks for fattening purposes.

For laying purposes, some first-generation hybrids in poultry are well known. The hybrids between R.I.R. and Sussex are excellent, where the market does not discriminate against a yellowish egg. The same is true of the excellent hybrids between Australorp hens mated with Leghorn males, and of the Barnevelder-Leghorn cross. In these crosses we see some of the best examples of uniformity and absence of "culls". Whereas it is usual to find a certain proportion of pullets in every breed which do not do well and which have to be scrapped sooner or later, mortality in the hybrid lots is exceedingly low.

A very interesting problem is raised by the facts found in the production of hybrids between breeds for utility purposes. Whereas at first many authors claimed that it was very important that for the production of such hybrids only the very best strains of highly-bred animals were used, it is found repeatedly that the choice of the breeds to be crossed is much more important than the strains in those breeds. For ordinary purposes the quality of the Barnevelder and the R.I.R. crossed are not very relevant.

The explanation probably is that the difference between a good strain and a poor one lies in the presence of many impurities in the strain. When the strain contains many individuals that are impure for different valuable genes, too many birds are produced that present diverse defects, and the better strains either contain fewer individuals impure for the same genes or no heterozygosis for several of them. When two strains are crossed and when those two strains "click", in other words, when the impurities in one strain are covered up by homozygosis for those same points in the other strain and vice versa,

it does not matter much whether we choose a poor strain or a good one, the hybrids will be universally good anyhow.

It is probable that the production of first-generation hybrids between different breeds can be utilized commercially much more frequently than hitherto. A drawback of the practice lies in the possibility that the users of the hybrids will be so struck with their good qualities that they will use them for breeding purposes; and as those hybrids are impure for all the genes in which the germ-cells differed, their offspring are so very variable and comprise so many defective and inferior individuals, that the average quality is exceedingly low.

In swine, for instance, there exist so many impurities in the breeds, so many genes for which many of the members of even the highly-selected breeds are heterozygous, that cross-breeding even very closely-related breeds to produce animals for use is a recommendable breeding practice.

In hybrids between the German Landrace and Large White Yorkshire swine, the uniformity of the groups is very striking, and in the hybrid lots, poor doers and backward pigs are exceedingly rare.

When, however, an F2 generation is raised by mating such hybrids among themselves the result is astonishingly bad. I have seen a number of litters of such pigs from hybrid parents, and the first thing which strikes one is that no two piglets are alike. So many of the animals are unthrifty, so many show the effects of all sorts of small aberrations, that a really good pig in such litters is a rarity.

I have raised large numbers of chicks from hybrids between the Leghorn and the Barnevelder breed, and although the two strains crossed were excellent and the hybrids themselves were remarkably good, the second generation showed so many poor hens—hens that did not lay before they were ten months old, or that laid a dozen eggs, or no eggs at all, hens with crossed beaks, weak chests, crooked spines, poor feet, bad eyes, and all sorts of minor aberrations—that in this generation only a very few hens were passably good.

NOTES

This is an interesting chapter which Hagedoorn might well have expanded considerably as a result of more recent developments in poultry breeding. Never-

theless, the chapter as written contains the gist of the matter. Since many first generation crosses between two breeds are more uniform and more productive than either parent breed, and, what is perhaps of greatest importance, more resistant to unfavourable environmental conditions—in other words, hardier—the importance of such first crosses or hybrids in all branches of animal husbandry is likely to expand. Since, in the first place, there must obviously be sufficient numbers of the two breeds to cross, the possibility of the commercial utilization of first generation hybrids is clearly related to the prolificacy of the species concerned, being greatest in poultry and in swine. As regards the theoretical explanation, I doubt whether many modern geneticists would accept Hagedoorn's simple yet convincing interpretation as being the whole story. From the practical standpoint, however, the precise genetical significance of hybrid vigour is of minor importance.

Hagedoorn's warning against the temptation of in-breeding first crosses because of their uniformity and productive superiority is one which I can confirm from my own experience. Both uniformity and productive superiority are very apt to go with the wind. It would require many generations of strict selection to bring them back. Personally, I have doubts as to whether, in their entirety, they would ever come back.

Chapter Fourteen

Grading Up

When a breed is imported into a new country, it may be found that it possesses advantages over existing breeds sufficiently great to make it economically important to substitute the new breed for the old.

When we are dealing with very fertile animals, such as poultry, ducks or swine, this is a simple matter as we need only multiply the new breed up to a point where it supplants the existing breed.

In the larger farm animals, however, this is not feasible. In cattle and horses it is generally found that a man who possesses a certain number of female animals must reject so many of the young, that he can only with some difficulty replace every cow by one daughter, every mare by one filly. This is especially true in herd-book cattle; in most herd-books the cows exist only for about four or five years as registered animals, so that they only average one daughter each.

For this reason it is not possible to import a herd of cattle or a breeding group of horses, multiply the group, and make them supplant an older breed. The only economically possible way to supplant an existing breed with a new one is by "grading up" the old breed into the new.

The way to do this is to cross females of the old breed with males of the new one, to cross the hybrid females so produced with males of the new breed, and to continue this process. If we stop using males of the old breed, and use only males of the new one, it takes only a few generations of crossing to make the herd change over from the old level to the new. In four or five back-crosses most traces of the old breed are lost, and the herds consist of fairly representative members of the new breed.

The genetical explanation of what happens during the process is of some importance if we want to understand the process to change it where necessary. When we are changing one breed into another, we hardly ever know the genetical constitution of the two breeds; but we are sure that in regard to a great number of genes the breeds are identical, while they differ in a number of others. The genes for which all animals in both breeds are pure remain untouched during the change. As regards the other genes, however, the new breed may possess a number of genes that are lacking in the old one, or vice versa. Let us first take the case of a gene that is present only in the new breed. The first hybrids between the breeds will possess this gene, but they will be impure (heterozygous) in regard to it. To take a concrete example: when we are breeding a horned breed of cattle to a polled breed the hybrids will be polled. They will be impure for the gene in question, *Pp*. When we are crossing those hybrids back to pure males of the polled breed (*PP*), we have the cross $PP \times Pp$. Half of the germ-cells produced by the hybrid will have *P* and half will lack it; but the pure polled parent (*PP*) will give factor *P* to all its offspring, and consequently half of the back-cross animals will be pure (*PP*) and half will be impure (*Pp*).

This is true of every gene that is present in the new breed and not in the old one. Let us suppose that we are crossing polled Angus cattle, which are polled and black, to red Shorthorns. The hybrids will all be polled and all black, but they will be impure for two genes, *Pp*, *Bb*. They will make four kinds of germ-cells, *PB*, *Pb*, *pB* and *pb*, whereas the pure polled Angus bull will make all *PB* sperms. The result will be that all the back-cross animals will be polled and black, but one half will be pure for *P*, one half impure, *Pp*, and at the same time one half will be pure, one half impure in regard to *B* (*BB* and *Bb*).

The same is true of every gene that the new breed has more than the old, and the consequence of this is that the chance that one particular daughter of a pure-bred bull in any back-cross generation will be pure for one of these genes is 50 per cent.

This means that when the two breeds differ in a great many genes, and when we compare one animal to her daughter in any generation, the daughter will be pure for half the number of genes in which her mother was still impure, or in other words, the impurity is halved in every generation.

The same is true in regard to all the genes which are present in the old, but absent from the new breed. If the new breed lacks a factor A which is present in the old breed, the first generation are all Aa. They will make two kinds of germ-cells in regard to A, 50 per cent. with A and 50 per cent. without A. This means that 50 per cent. of the young of the first back-cross generation will still have this gene, 50 per cent. will lack it. It can be seen from the foregoing that both in regard to genes that are present in the new breed and to genes that are lacking in the new breed the same is true—the number of genes in which the back-crossed generations are still different from the new breed is halved in every generation.

Thus, in a very few generations, repeated back-crossing will transform any breed into any other breed with which it can be crossed. If originally the breeds differed in 32 genes, the hybrids will be heterozygous for all of them, but one back-cross animal will only be impure for 16 genes, *her* daughter will only be heterozygous for 8, *her* daughter for 4, and so on, so that complete purity will be reached in this case in six generations. This is so when no selection is practised; with selection the transformation of the original breed into the new one is considerably hastened.

In all instances of this kind we are simultaneously dealing with genes that the new breed possesses, and with genes that it lacks, as compared with the original breed. Whereas purity is progressing at the same rate, there is this difference between the two groups of genes: we can see the presence of genes that are derived from the old breed, but we can hardly ever see the impurity for genes which the new breed has more than the old one.

Generally, when two breeds differ in very many points, there is great probability that an approximately equal number of genes that differentiate the two breeds will be present in each of the breeds crossed. This is important, if we want to judge the purity of the back-crossed animals, for instance, when we are debating their registration in a herd-book.

As far as the genes are concerned which are present in the original breed and not in the new one, and which therefore must be eliminated, we can see the effect of those genes upon the quality of the back-crossed animals. Purity, however, is progressing equally in regard to both sets of genes. For this

reason we can use resemblance to the new breed as a measure of purity. When the back-crossing has progressed so far that the graded animals have become typical representatives of the new breed, we can be reasonably sure that they are pure in regard to their genotype, and we need not hesitate to take them into the registered herds.

This process of repeated back-crosses to a better breed is extremely useful in animal breeding. By its means we are able to transform a large group of animals of one breed into a wholly different breed in a few generations, and when we are dealing with polygamous animals we need only a very few males for this work.

When at the beginning of the first world war a number of outstanding Belgian breeding stallions came to Holland into safety, those stallions were used in the provinces of Zeeland, Brabant and Limburg to grade up the local horses. In very few years the horse population, especially in Zeeland and in Limburg, was transformed in this way into excellent Belgian pure-bred breeding stock. It would have been absolutely impossible to multiply the few pure-bred Belgian horses in Holland and make them supplant the local horses in less than two centuries. In the way described the work was practically finished in ten years.

It must be emphasized that this process of changing an existing breed into a wholly different one by repeated back-crosses is one that goes on with great regularity in an automatic way. Selection of individuals resembling the better breed will help somewhat to hasten the work, but it must be remembered that even without any selection, repeated back-crossing to one breed will change the population into that breed automatically with great rapidity.

Grading up is the cheapest way of changing over the population of a certain kind of animal into one definite approved breed: but it must be noted that there is one drawback to this system of breeding—the only thing that can easily be accomplished by it is a complete change of one breed into one definite other breed. It is almost impossible to stop half-way. When we are specially struck with the excellent quality of the cross-bred animals, we will not be able simply to stop there and make a breed of animals that will show those excellent qualities of these hybrids; we must go on to reach a condition when the animals

will breed reasonably pure, and this condition will not be reached until the complete transformation into the new breed has been accomplished.

It is very important to bear this in mind when we are proposing to ameliorate an existing breed of animals by crossing it with some other imported breed; for if we know that the only way to make a success of the "grading up" process is to continue it all the way, this means that before we begin we must know that the new breed, such as it is, is wholly satisfactory to us.

For example, when we propose to change a small breed into a breed of larger animals and when we want to do this by means of repeated back-crosses with a large breed, we must know that the size of this large breed in its pure state is just the size we want our animals to attain in future. We cannot stop by the way, we must go on until the population is wholly transformed into the new breed with all its original qualities, good and bad.

NOTES

This is all very sound, although I do not think that in this case the introduction of elementary genetics has made the argument any plainer, rather the reverse. As Hagedoorn rightly says: "Grading up is the cheapest way of changing over the population of a certain kind of animal into one definite approved breed." There are certain biological advantages in addition to the economic one of cheapness. It is the safest as well as the cheapest, since many of the advantages of acclimatization and disease resistance of the original stock may be at least partly retained.

Hagedoorn gave a clear warning as to the main danger of up-grading. "It is almost impossible to stop half-way." In general the first cross gives a fairly clear guide to future policy. If there is *to be an advantage in up-grading, then the first-cross progeny should be outstanding since they benefit from hybrid vigour as well as from the up-grading. If they are not outstandingly superior, stop then, for the results from further up-grading are likely to be worse rather than better. If, on the other hand, the results of the first cross are encouraging, then continue, "until the complete transformation into the new breed has been accomplished."*

Chapter Fifteen

Small Groups

For one reason or another it may happen that a group of animals consists of only a few individuals, and it frequently happens that the opinion of a geneticist is asked by breeders who have to decide just how to deal with such small groups.

This case may perhaps be best illustrated by a few examples that have come to my notice, so chosen as to comprise instances of the most diverse kind.

Of the several causes of the existence of numerically small groups, the most obvious ones are those in which the group consists of the remnants of an old breed or of an old, almost extinct species, and the opposite instance in which a new breed has recently been created.

At first sight it appears as if a small group must always be handicapped by its small numbers. In a larger group there is more scope for selection. In a large group, especially in a very widely-bred variety, there is more chance of the adaptation of sub-groups to the most diverse circumstances, and it is quite possible that a very small group may for some reason disappear altogether. There are, however, a few advantages that every small group has over any of its rival and much larger groups. In the first place the very small number of individuals in such a group causes a rapid reduction of its potential variability. From a commercial point of view, the very rarity of any new or old breed or species may cause such a relation between demand and supply that the few individuals that comprise the breed are eagerly sought after and bring a relatively good price.

A newly-created breed is an instance of this kind. When we produce a new breed of poultry, or pigeon, or dog, this breed,

provided it has reasonably good qualities, will almost always be eagerly sought. The breeders have only a few animals to dispose of, and can afford to wait for a few customers who will be willing to pay a stiffish price. In this respect a newly-made breed or a newly-imported breed will be profitable to their breeders for the same reason. This is especially noticeable with dogs.

It would seem as if there were an enormous difference between instances in which a group of dog lovers established a breed society to save a valuable local breed from extinction, and others in which another group came together to manufacture a new breed. From the following examples, however, it will be seen that such instances are nevertheless very similar.

Around 1935, a number of dog lovers in the province of Friesland got together with the object of saving their two local breeds, the Staby and the Wetterhoun, from what they thought was certain extinction. Those breeds are closely alike, the Staby being smooth coated, the Wetterhoun curly coated, and both are used as farmers' yard-dogs, and as hunting dogs. The Staby is more common in certain villages, the Wetterhoun in others. Separate stud-books were started, and very rigid score cards were drawn up, in which the distinction between the spaniel-like Staby and the curly-coated coarser Wetterhoun was emphasized. When the men consulted me, I tried in vain to convince them that it would be ever so much better to let the visible qualities of the dogs take care of themselves, to breed for usefulness, for intelligence and hunting prowess, and I prophesied that if they simply registered every dog that went by the ancient names, and restricted the choice of males to a few outstanding ones, the "type" of the breeds would take care of itself.

It was very curious to note after ten years, that the most numerous of those two Friesian dogs, the Staby, which was in the hands of a great many show breeders and city men, notwithstanding its being selected for "Type", has become (or remained) exceedingly variable. The Wetterhoun, on the other hand, being in the hands of relatively few specialists, who hunt polecats with those dogs in the dark of the night, has been selected strictly for work, and only a few famous hunting dogs have been used at stud. Compared to the more numerous breed, the Wetterhoun has become very much more of a fixed type during those years, and comparatively speaking we now have one very typical and useful water dog, the Wetterhoun, and a

very variable second lot of dogs that go by the name of Staby. Part of this difference in results is certainly due to better selection in the one instance, but I am convinced that part of the difference in results is simply caused by the circumstance that fewer males have been used in the Wetterhoun in every generation.

Whereas in those two breeds, just as in the Corgy in Wales, we were dealing with a multitude of dogs of rather variable type in the hands of a great many small breeders who had been breeding those dogs at their farms for a very long time, it sometimes happens that dog-loving enthusiasts want to re-establish a breed that has in reality disappeared as such. A very good case in point is that of the Dutch Sheep-poodle. Where overpopulation and the resultant pressure upon agriculture has not yet crowded out our shepherds and our flocks of sheep in Holland, those shepherds often used a smallish, shaggy, bobtailed sheepdog, more or less like a miniature English bobtail. Now the sheep flocks have gone as long ago as fifteen dog-generations at least, but those dogs still live on in the memory of those of us who have known them. Evidently the breed itself has disappeared as such. Nevertheless, it often happens that we meet an occasional mongrel dog that happens to show some of the qualities of the old sheep-poodle, although it must be evident to anybody that there is hardly any possibility that such occasional dogs have really descended in any direct way from the old sheep-poodles.

In 1946 a number of dog lovers in Holland came together, mainly at the instigation of one of our show judges, Mr. Toepoel, to save (or to re-make, according to me) that old national breed. Those dog owners all had one or a few dogs they had found and bought in the most unexpected places, in towns, in villages, at cattle markets, dogs that reminded them of the old sheep-poodle. One day they were proposing to follow the ordinary routine, to incorporate as a breed society, to establish a score card for judges of the breed, and to make a herd-book section for this dog. This time I happened to be present at the right moment, and the result after a few meetings was that the owners of those dogs followed my advice. They have established a herd-book and register in which they simply register a limited number of dogs without any selection at all, namely, all those dogs that are called "sheep-poodles" by their owners. I counselled

them to close the register as soon as about thirty dogs are inscribed, to register only pups bred from the present dogs, reduce the number of males in the breed to as few as possible, three rather than six, but one rather than three, if they can agree upon the individual, and to leave any score card till the moment when out of the present chaos a fixed type will have evolved. As a geneticist (see the chapter on the reduction of variability) I could promise them that automatically the breed would obtain a set of qualities of its own, and if the breeders really choose an occasional male according to his mental qualities, intelligence, obedience, good behaviour, they will very soon have a valuable new house-dog with its own peculiarities, and a great future. It will be extremely interesting to see the results of this experiment, and we can only hope the breeders will have the strength of mind to see it through during the first three or four critical years.

Whenever any old breed or any species of animal for any reason has come down to a few dozen pure-bred specimens, we must inquire what is the correct way to save this breed from complete extermination. Sometimes the number of pure-bred individuals is really very small indeed. A very curious example is that of a few deer that only survived in the yards of one single monastery in China. In this instance a very few specimens survive in zoological gardens, so few, indeed, that complete extinction of the species seems certain.

This is not always so, for it may happen that just in the nick of time some few enthusiasts co-operate to save the group. A very good example is that of the American bison. When it seemed as if this species was doomed to survive only as a series of small groups in zoological gardens, the U.S.A. Federal Government stepped in. To-day several big herds of this animal have been established in suitable surroundings, and the danger of extermination is well past. On the other hand, the survival of the European bison is by no means so certain. During the second world war the last wild animals of this species were killed, and the species only lingers on in a few zoological gardens. When, some years ago, I discussed the status of the European bison with some of the people responsible for its survival as an inmate of our European zoological parks, I proposed cross-breeding with the more numerous American bison as a means of re-establishing thriving herds of this species. On this

occasion I found that although cross-breeding has been done at several places, and although the hybrids are fully fertile in both sexes, there was very strong opposition to this scheme. Sentimental reasons enter into this question to some extent, although in the long run we would be able to say with some truth, that after seven or eight back-crosses the herds would again have the real genotype of the European bison. We must also, however, reckon with economic reasons. The very fact that pure-bred European bisons are very, very rare, makes it extremely profitable for any zoo to produce pure-bred ones. Several zoological gardens have combined and established a hermetically closed herd-book society that is able to guarantee the unmixed ancestry of the very few surviving pure-bred animals. I am glad to say that side by side with this project, cross-breeding with the American species goes on, for it is really very doubtful whether the existing numbers of pure-bred beasts are sufficiently large to make a continued survival possible.

An interesting example of a very vigorous and excellent breed that exists in small numbers is that of the very oldest of the British horses, the Exmoor pony. This pony breed has been threatened by cross-breeding to some extent throughout its existence, and it is very striking how this breed of typical and singularly good-looking ponies has withstood all this. The only reason I can see for this is the fact that the numbers of Exmoor ponies have been small, while conditions of life in Exmoor forest have made survival of cross-bred stock, less well adapted to the extreme conditions, very problematical. Here is a smallish, very sure-footed, very good-looking and extremely sturdy horse, with very marked eye rings and nose markings, in build and colour very much like Asiatic wild horses, with smooth, tireless gait and capable of giving a grown man a good day's hunting, surviving in conditions of pasturage in which one would expect nothing better than a scraggy miniature. As the numbers of ponies and the number of owners are so small, a breed like this can only continue to exist if a few of those owners take enough interest in the breed to keep a small nucleus of pure-bred breeding stock intact. With all such old and valuable breeds the chances of survival are better if duplicate nuclei are set up in more than one locality. The example of the European bison, however, shows that even this splitting up of a small group may in itself threaten the breed's survival.

Financially, and in matters pertaining to propaganda and advertising, very small herd-book societies are at a disadvantage, and it often happens that they have to give up the struggle for life. Every time this happens the world is just so much the poorer. Breeds like Lord Bathurst's Gloucester cattle, and our Dutch Belted Lakenvelders, are very much worth conserving.

Amalgamation of separate herd-books that sponsor the same breed may sometimes be dictated by semi-political reasons, local jealousies and other things that have nothing to do with the quality of the animals. At first sight it seems better to have one strong breed society than two or three local ones. It is not generally realized that a herd-book group with only a relatively small number of bulls has the enormous advantage over any much larger group that the reduction of variability, with the same attention to selection, is much more rapid. The Friesland herd-book for black and white cattle in Holland is a provincial affair, while Holland also has a general herd-book for all the rest of the country with many more cattle. It would be a calamity if those herd-books amalgamated, as just now the small group of Friesland cattle acts as a nucleus for the breed and furnishes most of the very best breeding stock for the rest of Holland, as almost any pedigree of Dutch black and white cattle will show. In fact, I have repeatedly advocated splitting up the Dutch herd-books into provincial groups, separated by watertight partitions, to obtain a reasonably quick rate of purification in this excellent breed. The Groningen herd-book for white-headed blacks is very small, and it is in danger of being absorbed by the National herd-book society. Again, this amalgamation would be a serious loss for cattle breeding in Holland.

NOTES

An odd yet interesting chapter demonstrating the extraordinary and perhaps unique experience gained by Hagedoorn during his period of work as a consulting geneticist. It includes consideration of problems as diverse as the breeding of house-dogs and the preservation of the European bison and Gloucester cattle!

No author is ever completely consistent throughout a whole book. In certain examples of advice offered to dog-breeders, Hagedoorn seems to me to support the efficacy of selection by phenotype which he condemns in other chapters dealing with farm animals. He wrote, (p. 106) " . . . if the breeders really choose an occasional male according to his mental qualities, intelligence, good

behaviour, they will very soon have a valuable new house-dog with its own peculiarities, and a great future."

Perhaps it would have been more consistent with Hagedoorn's general teaching to have added, "but be sure to wait long enough to see how the first litters of puppies behave!"

Chapter Sixteen

Adding One Gene to a Breed

When we are changing over a breed into a second one by repeated back-crosses to good typical animals of this second breed, we have seen in a preceding chapter that the process is an automatic one which goes on and on until the transformation is complete.

Rapidly, purity is attained for all the genes that are present in the new breed, and the genes that were present in the old breed only are lost one after the other.

In a general way, it can be said that there is no way of arresting this process at any given point, but there is one exception to this: it is possible to retain one of the genes derived from the original breed, while transforming the mass of animals into the other one. In this way it is possible to add this one gene to the make-up of the other breed. We can take one single gene from any breed in which it is present and put it into the set of genes of any other breed.

A few examples will illustrate this process. In poultry there is one gene that has the effect of changing black colour into white and black markings into white ones. When I mated the White Leghorn with the Barnevelder, which has black markings on a brown background, the resulting hybrids were white in colour and intermediate in different respects between the two breeds crossed. When those hybrids were mated back to Barnevelders, half of the young possessed this white-marking gene, half of them lacked it. I now proceeded by retaining one or a few white-marked birds in every generation and mating them back to pure Barnevelders. As a result the animals gradually assumed the genotype of the Barnevelder breed. The hens commenced to lay dark-brown eggs, the comb, the general conformation

and all the characteristics of the birds became those of the Barnevelder breed. As, however, in every generation I chose only birds with white markings, the result was that in a few generations the colour of the animals became brown with white markings, and in seven generations it could be said that a new colour variety of the Barnevelder was created, the Jubilee Barnevelder.

When it is desired to produce a polled variety of some horned breed of cattle we have to proceed in this same way. Breeding our animals with some polled breed will give us polled hybrids, and breeding those back to our own breed will give 50 per cent. polled and 50 per cent. horned calves. By continuing the line from polled animals only and re-mating them to pure-bred animals of the breed to be dehorned, in six or seven generations we will have attained our end, the production of a polled variety.

Another example from poultry is that of the bluc breeds. When we desire to produce a blue variety of any black breed, the only thing we need to do is to cross our black breed with some blue one, and to breed back and back to the black breed from blue individuals. In this way some of my correspondents have produced Blue Cochin bantams and Blue Orpingtons, in every respect equal in quality to the black ones.

The last example I want to give is that of the auto-sexing breeds of poultry. I produced an auto-sexing Barnevelder, and an auto-sexing Leghorn by adding the so-called "barring" factor to the Barnevelder and the Brown Leghorn respectively. In this breed the effect of this added gene is the possibility of recognizing the sexes at birth.

When, at the end of a series of back-crosses, we have succeeded in producing animals that are equal to pure-breds of our original breed with the exception of the one factor added, we must remember that all those individuals are heterozygous. As in every generation we have mated a heterozygous animal (*Aa*) with one without this gene *A*, all the animals showing the gene *A* are heterozygous, impure, for *A* (*Aa*). When we want to "fix" this character in the breed, we will now have to produce a number of homozygotes. The way to do this is to mate heterozygotes together. After producing a number of Jubilee Barnevelders which all have had one brown parent and which for this reason are all impure (*Aa*), we have to mate those animals together. This will give us a number of animals in which out of

every four three will show the presence of the gene, and only one will lack it. The next move is to find the homozygous animals. The breeding together of $Aa \times Aa$ will give us a proportion of one AA to two Aa and one aa, and the difficulty now consists in distinguishing the AA birds from the Aa ones. This we can best do by test-matings. That is to say, we mate a number of white-marked birds with brown ones. If we do this we will find that most of them will give both white-marked and brown

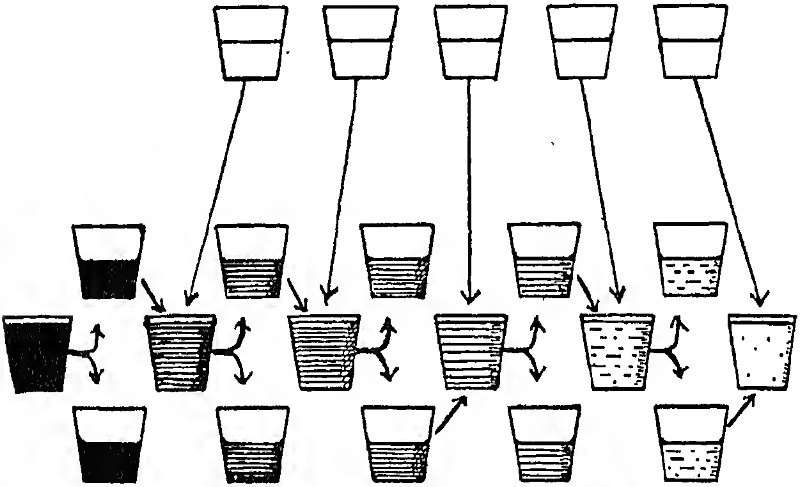


FIG. 12.—A simple classroom experiment to illustrate "grading". A tumbler of coloured liquid (or preferably coloured seeds, such as beans) representing a specimen of one breed, is emptied into two similar glasses (representing germ cells). One of these is rejected, the contents of the other one are combined with one of several tumblers half-full with colourless liquid or white beans, representing germ cells of the second breed, to form the hybrid generation. The process is repeated until the liquid is colourless or until all the beans happen to be white.

chicks, but that there are a few that from such test-matings will give white-marked ones only ($AA \times aa = 100$ per cent. Aa; $Aa \times aa = 50$ per cent. Aa and 50 per cent. aa).

When next we continue breeding from the homozygous birds only, from those birds which when mated to brown gave nothing but white-marked chicks, we have fixed factor A into the new breed once and for all.

In the same way there comes a moment in the dehorning a breed of cattle when we will have to breed polled ones together, and to test-mate the resulting polled calves in order to find the desired homozygous PP ones.

In many instances in which we make use of this system in adding one factor to the make-up of an existing breed, fixing the breed will not be necessary. There would be no real object in producing a pure-breeding strain of Jubilee Barnevelders; the white-marked animals are bred for show purposes only, and they

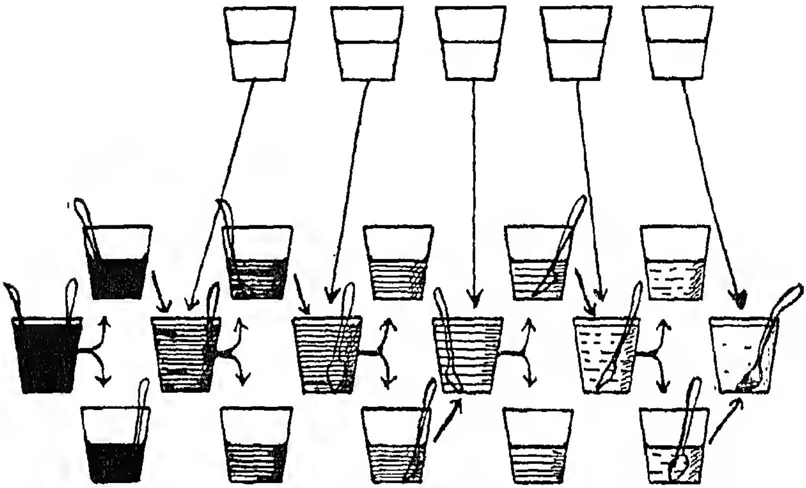


FIG. 13.—An experiment illustrating the adding of one gene to a breed. Everything is arranged as in Fig. 12, with the exception that a spoon is placed in the first tumbler. When the contents of the glass are divided over two glasses, the spoon is present in only one of them. At every division the tumbler containing the spoon is chosen and the other one rejected. The experiment is continued until the spoon is standing in a glassful of exclusively white beans.

can very well be mated with ordinary black-marked ones in every generation.

Adding one single gene to the make-up of an existing breed is really of the greatest use in producing novel show breeds in such animals as dogs, poultry, rabbits, etc. Only in rare instances will it be really economically important to add just one gene to the make-up of an existing breed.

NOTES

In this chapter the geneticist gets down to his conjuring tricks with the aid of a useful lecture table illustration. In the last paragraph, Hagedoorn is delightfully frank concerning the practical utility, or rather the inutility, of this particular trick.

Chapter Seventeen

Breeding-out Recessive Qualities

The more I see of pure-bred stock, the more it seems important to me to tell the breeders how to get rid of undesirable impurities. One of the main reasons for the indiscriminate cross-breeding we meet in all sorts of livestock is the fear of "degeneration" by in-breeding. Every time I talk to breeders I find that what they are most afraid of is the birth of typically inferior individuals, malformations in poultry, weakness in foals, blindness in dogs, hernia or *atresia ani* in piglets. Observant breeders all know that such aberrations are much more frequent when relatives are mated than when the male used is quite unrelated to the females.

It is not surprising if such observant breeders, anxious to avoid trouble of this kind, go to the other extreme, and choose a male that is sure to be unrelated, if necessary a male from some other family or even some other breed. The popularity of the Hampshire Reds in the years after the second war (I am now speaking of England and Holland only) is mainly due to the fact that the breeders of Rhode Island Reds use them to "ameliorate" the R.I.R. stock. I am very glad to say that many progressive breeders are nowadays beginning to realize the danger of such cross-breeding, which produces a high degree of heterozygosity in the stock.

Breeders of sheep, water buffaloes, fowls and ducks, who are starting closed nuclei in many countries to bring the average quality of their stock up, often have great difficulty in finding foundation stock that have been highly selected and close-bred for a good many generations, but even when they find such material it is generally still giving all sorts of culls. Almost always such culls are individuals deficient in important genes.

There is no clear-cut line of demarcation between cases in which the embryo or new-born animal dies because of such a deficiency, and those in which some "bad doers" are occasionally born. When anyone starts in-breeding with stock that have not been in-bred before, the production of unfit individuals is the rule rather than the exception. In fact, this is how some of us obtain most of the aberrant stocks with pathological abnormalities, like Hammond's thin-haired rabbits and dwarfs, and my blind pigeons and epileptic animals.

This impurity in regard to very important, vital genes, as well as for genes that help to bring about typical racial characters is a subject that we consulting geneticists know only too well from the experience of the breeders who ask our advice. It is astonishing to see how often even males with pedigrees of great length are shown up as heterozygotes, Friesian bulls that give dun-coloured calves, Essex or Wessex boars that give solid black or "trippling" piglets, Redpoll bulls that, when mated to cows of another breed, are shown to be heterozygous in respect to horns or spotting or even both, famous stud dogs siring blind or deaf or deformed pups, or pedigree cocks that give rise to deformed or very weak chicks.

The question that is often asked is just how to rid the strain, or even the whole breed, of such hereditary faults.

On paper, this question is not difficult to answer. Elsewhere in this book (p. 146) we have discussed how sometimes it will pay to test-mate a number of breeding animals by means of deliberate matings to partners that lack the important gene. A very good example of a case where this has been actually done by some breeders is that of the single-comb Wyandottes. However, the matter is seldom as easy as this, and even in the simplest instances it may be practically impossible to use the method of direct test-matings.

What we need is a method that can be safely applied in every instance, and which is so designed as to reduce the proportion of handicapped young stock born, from generation to generation.

I think a few examples in which I was consulted may best illustrate both the principle and some of the peculiar difficulties. In some breeds of dogs it sometimes happens that a few pups develop blindness, and in at least two other breeds pups often become stone deaf. In both examples it is evident from the

pedigrees and from analogy with very similar instances in human beings, as well as in rats, that we are dealing with inherited defects. With both troubles the abnormality is most frequent in certain "blood-lines", and it often happens that the first cases that come under our notice all trace back to some common ancestor. When such instances first come to the notice of a consulting geneticist, they tend to be already widespread, as at the outset the breeders do not think that defective heredity can be the cause. When an abnormality is seen in quite young animals the aberrant pups are simply killed and disappear. When they become more frequent the abnormality is seen to run in certain families in the way all recessive qualities do, that is to say that certain matings give abnormal pups and others never do, while in the beginning abnormal bitches mated to unrelated studs produce apparently normal litters.

In such instances the remedy that seems obvious is test-mating. To be sure that an individual pedigree dog is homozygous in respect to the gene the blind (or deaf) dogs are deficient in, all we have to do is to mate him or her to a few of the abnormal animals, for if such matings give only normal pups the tested individual is free of the "inherited taint". In theory we could establish a group of tested homozygotes that would be guaranteed free.

I have had numerous discussions with individual pedigree breeders and stud-book officials on the subject, and I have come to the conclusion that this is not at all what I could recommend. There are several reasons for this. It so happens that blindness occurs in three separate breeds of show dogs, and hereditary deafness in two others in a certain group of breeds very popular with handlers and exhibition breeders. A breed society sponsoring one of those breeds would almost certainly injure that breed in the public view by the mere fact of openly discussing ways and means of breeding out a serious defect like progressive retina degeneration. The dog-buying public would simply turn away from that breed with all the blind pups, and patronize some other and very similar breed in which no talk about blindness has yet leaked out. Again, think of the number of pups, slowly getting blind, that would have to be deliberately produced to test-mate several studs to blind bitches, and especially of the number of valuable fashionable show bitches that would have to be test-mated to blind studs. Would we be sure

that all the perfectly normal full-grown pups born from one blind parent, would be killed or castrated?

I have thought of a quite different way out of the difficulty, and seriously recommend it to all the breeders of dogs in which such hereditary deficiencies occur, but especially to kennel-club councils in every dog-breeding country. This plan is based upon Wriedt's scheme of testing studs.

Wriedt, in his admirable Norwegian animal-breeding book, proposed deferring the granting of final registration certificates to males in agricultural animals until such studs had been mated to a specified number of their own daughters and had been shown to give no abnormal or grossly-inferior offspring from such matings. Without going into the merits and demerits of this scheme in respect to all species of domestic animals, I only desire to point out here that it offers a very satisfactory way out of the enormous difficulties met with in certain groups of animals, notably dogs and pigs.

With dogs it would be quite feasible to establish a voluntary registration scheme for stud dogs, quite apart from and in addition to the usual registration system. Such a registration scheme would have to be open for males of all existing breeds, and anybody should be free to propose or not to propose his valuable stud dog for the granting of the special certificate. This certificate should be granted to a pedigreed male dog, that had been siring a given number of litters, or a certain number of pups from matings to his own daughters, when inspection of these inbred pups had shown them to be all free from defects due to a deficient genotype. In establishing such certificates, the governing body, breed society or kennel club, should carefully discuss the advisability of naming specific defects, such as deafness, dwarfness, retinal atrophy or night-blindness, undershot jaw, cleft palate, cryptorchidism, claustrophobia, etc. Very good reasons could be adduced, I think, for leaving this to the discretion of the inspectors appointed.

If application for the certification were left optional, it might be that breeders of Poodles or Boxers or Chows, would use the scheme to certify homozygous studs in respect of inherited defects altogether different from those considered by breeders of Setters or Spaniels. I venture to suggest that those who know would soon patronize the certified fashionable studs, in Setters as well as in Poodles, in Airedales as well as in Chows.

Show breeders of dogs are for obvious reasons not very anxious to advertise the fact that some of the most fashionable studs in the breed they sponsor are heterozygous in respect of important genes every normal dog should possess (carry recessive lethals, to use a semi-genetic phrase), and for those same reasons I have refrained from attributing particular defects to particular breeds in which I know them to occur. The beauty of Wriedt's scheme is that it would soon show the dog-breeding public which studs were safe to use, even without recourse to such obviously hypocritical measures as declarations of freedom from recessive traits asked from the owners at the time of registration. A voluntary general certification scheme to be established for all breeds would be entirely satisfactory. The patronizing of males of tested purity may not seem a very radical measure, for obviously it would leave the bitches untested, and it would have to be done over and over again during several generations. It is, however, a very sound scheme, for a continued use of homozygous males only will in a very few generations bring down the incidence of abnormal births to almost nothing.

In such animals as pigs and dogs individual males have an enormous influence upon the next generation. If it is possible to use proven breeders, males that are certainly homozygous in respect to a gene we want all the individuals to have, the proportion of their offspring that are still impure will be only 50 per cent. of that of the preceding generation. Every homozygous female used will produce 100 per cent. homozygous young, and every heterozygote will give as many pure as impure. If 10 per cent. of the population are heterozygous (*Aa*) and the rest homozygous (*AA*), a homozygous male mated to such females will produce a group of daughters of which only 5 per cent. will be heterozygous, and so on from one generation to the next. In the meantime such proven homozygous males will never, even from heterozygous females, give any aberrant (*aa*) young stock.

I have elaborated the case of harmful recessive deficiencies in the dog, and the quickest way in which they can be eliminated. In other, and economically more important, animals test-mating males to their own daughters is of the greatest utility when the potential variability in the stock is low (in other words when the stock has been selected and pure-bred for a long time). As long as there is plenty of variability, as in breeds in

which much cross-breeding has been practised (in cattle, sheep and poultry), the ordinary system of progeny-testing males by mating them to a good random sample of females that are not necessarily related to them, is good enough (and gives quicker results). When, however, we are dealing with rare and at the same time serious aberrations, the proportion of heterozygotes in the breed may be so low that only matings to closely related groups of females will help us to recognize the "carriers of the recessive trait". In such instances it certainly pays to stamp out the taint before it has made too much headway.

NOTES

Chapters Seventeen and Eighteen deserve the most careful study, and one does not require to be a geneticist to appreciate their importance. Everyone concerned with animal husbandry is aware of the frequent occurrence of what is somewhat vaguely termed a "bad doer", the animal that eats but does not grow; that succumbs to parasitic infestation where others in the same flock or herd continue to thrive; a loss to keep yet a puzzle to dispose of. Admittedly many of such "bad doers" are the result of ill-nourishment or accidental infection in early life, yet they are more frequent in some lines of breeding than in others; more common among the progeny of certain sires than in that of others. Undoubtedly, hereditary factors are involved, and as regards those hereditary factors Hagedoorn was right when he wrote:

"There is no clear-cut line of demarcation between cases in which the embryo or new-born animal dies because of such a deficiency, and those in which some "bad doers" are occasionally born."

Without being unduly specific concerning the hereditary factors involved or the hypothetical mechanism of their inheritance, it is obvious that before any sire is used extensively it is really essential to be as certain as is humanly possible that he leaves stock that does *thrive and is without recognizable defects in any character of economic importance. With the development of A.I. the importance of taking such precautions has enormously increased.*

The Norwegian geneticist, Wriedt, advised test-mating a sire with a specified number of his own daughters as means of detecting any such hereditary defects, and Hagedoorn whole-heartedly agreed with that recommendation.

It seems to me that other authorities interested in livestock improvement, in paying less particular attention to the advisability of such methods of preliminary test-mating of sires destined for extensive use through A.I., are accepting risks which, in view of genetical knowledge, need not and indeed should not be accepted.

Chapter Eighteen

Lethal Factors

In many domestic animals and birds, embryos are often produced that have not the required inherited quality for a complete normal development, and sometimes young animals are born alive that are destined to die young.

To give a few examples I might begin by pointing out the frequency with which in litters of swine one or two weaklings are born that never do well, and are mostly killed as soon as recognized. The fact that this sort of thing occurs frequently should not be taken as proof that we are dealing with accidents during pre-natal life, as the same sow that will produce a few of these weaklings when mated with a boar of her own breed will never produce such aberrant young when she is mated with a boar of a different breed. Crested canaries mated together will always produce a few young that die as soon as hatched, because the top of the skull is defective. In ducks exactly the same thing is found.

Among cattle the best-known lethals are bulldog calves, such are always born in a certain proportion of instances when Dexter-Kerries are mated together. In sheep and goats, young with abnormal feet and legs, or with abnormal sexual organs, are often produced in certain breeds. In sheep I saw a curious family of cross-bred sheep on the island of Wieringen some years ago in which the legs seemed amputated. These lambs were produced by one ram when mated with his mother and sisters.

In horses, foals are sometimes born with atresia ani, an aberration in which the gut ends blind, so that they die in one or two days. In mice, rats and guinea-pigs I have seen many diverse cases of lethal genotype among the young.

Different categories of breeders attach more or less import-

ance to the production of aberrant offspring in their animals. The pedigree breeders, who are out to sell breeding stock and to register their animals in herd-books, are very apt to minimize the importance of lethals. It hurts business to recognize the importance of those things, and nobody forces these breeders to publish the birth of aberrant young animals—which simply disappear, the breeder trying to forget all about them. The value of a few outstanding animals produced by pedigree breeders over that of the second-rate ones born from the same parents is so great that one or more totally worthless animals among a great number of almost worthless ones is no great loss.

Ordinary breeders, however—the majority of users of the stock—attach much more value to absence of lethals, as the production of dying foals instead of saleable ones, or bulldog calves instead of healthy ones, is simply so much economic loss. It is time for the ordinary run of animal users to realize that it is relatively simple to purify the breeds of domestic animals in regard to such defects, so that they can force the pedigree breeders to give sufficient attention to the subject.

Breeders of swine are not at all surprised when two or three piglets in a litter are defective. One may be born eyeless, another may have a hernia, or thick, stiff forelegs, or no anal opening, or a piglet may be simply silly or unable to stand up, or one may keep squealing—it is "unhappy inside" as some pigmen say. It is very significant that a sow which, when mated to a certain boar, produces a few of such wasters, when mated to another boar, especially to one of a different breed, will not produce anything but healthy, normal piglets.

In poultry lethal factors may be responsible for many chicks dead in the shell. This is of not much account to a pedigree breeder, but it may be a source of considerable economic loss to the hatchery-men. Here again, it is significant that the same hens which produce a lot of eggs yielding "dead in the shell" chicks, when mated to a male of a different breed will give almost none of these non-hatching chicks.

In all those cases we are dealing with the same sort of thing that is also responsible for the birth of red calves in a black breed of cattle, or for the production of black lambs in a white breed of sheep, namely heterozygosity in respect to an important gene. This can be seen from deliberate experiments, such as I have been able to make with my small laboratory animals, but

also from the proportion in which such aberrant young animals are produced in the matings that do give them. In almost every instance this proportion is the Mendelian monofactorial proportion of one in four. In a few instances, especially where the lethals are first produced immediately after a cross, the proportion is much less, probably one in sixteen.

In all the cases where aberrant young with lethal genotype are often born, we must recognize that we are dealing with heterozygosity; part of our best stud animals must be heterozygous for important factors, so that half of the germ-cells they produce lack such factors, and produce aberrant young when they happen to fertilize germ-cells from equally heterozygous females.

Most breeders know very little about genetics, and they are apt to think a bull that gets a red calf very rarely is not as bad as one that has got very many red ones. They are apt to believe that as hernia in pigs is rare, a boar that gets just a few piglets with hernia is not very much to blame, and should be patronized by the pig breeders if the quality of his normal offspring is good.

In reality we should remember that in such a bull or in such a boar one half of his germ-cells only are of any value, the other half being worthless. If such a male is patronized extensively, he must give 50 per cent. of impure daughters again, among those that are not personally aberrant.

Wherever progeny tests are made to examine the quality of the offspring of apparently good males, they should always be utilized to recognize the males heterozygous for such vitally necessary genes as distinguish normal animals from aberrant ones. If the heterozygous males are not recognized, or if their impurity is glossed over so that they keep on producing a great many offspring, they can do an enormous lot of harm to the breed.

How is it possible to guard a breed of animals against the bad influence of sires heterozygous for vital factors? We must remember that in the ordinary course of breeding we may not recognize a heterozygous sire at all. The impurity may be new in the breed and due to cross-breeding or to a mutation, and in this event all or almost all females are homozygous, so that when mated with the heterozygous sire their offspring are normal. In such a case the male, when unrecognized, may spread

the impurity far and wide in the breed (half his children are impure!).

How can we safeguard ourselves against such a thing? The very best test for breeding quality in a sire is derived from the result of mating him with a number of his own daughters; for if a male happens to be heterozygous for a vital gene, half his daughters must necessarily be also heterozygous. If we mate him with a number of those daughters the matings with the heterozygotes must give 25 per cent. of aberrant young stock.

This test is especially adaptable to swine. Boars can have many offspring from their own daughters before they are very old, even before they are generally recognized as good or mediocre breeders. Mating a boar with half a dozen of his own daughters would surely bring out the fact that he was heterozygous for any of the vital factors, if such were true. In actual breeding practice the mating of a boar with his own daughters is often done.

Test-mating a sire with his own daughters is not only a good way to recognize heterozygosis in respect to vital factors, but it brings out every sort of impurity. If we simply examine the progeny of a sire it is possible that this animal is heterozygous for genes for which all the females he is mated with were pure, and this is especially true when a rare impurity is concerned.

In many animals it would be quite feasible to make a regular routine of mating all promising sires to a certain number of daughters. This could be worked into a system of official recognition of sires, or into a registration system. It would be possible to register males temporarily, but to defer official final registration until the moment we know that they did not produce any aberrant offspring from a certain number of daughters. The inventor of the system is the Norwegian Christian Wriedt, one of the first geneticists to understand the needs of animal breeding.

Chapter Nineteen

In-breeding and Out-crossing

To introduce the subject of in-breeding I would like to quote a few sentences I once overheard at a poultry show from a conversation between fanciers. A young man had asked what the difference was between in-breeding and line-breeding. An older one answered: "Well, son, it's this way: If you keep on breeding with your own birds, and you are successful, you speak of line-breeding. But if your results are bad, you can blame it to in-breeding."

In a scientific sense, in-breeding means the mating together of animals that are closer related to each other than random pairs in the group to which they belong. Speaking statistically, each animal or bird has two parents, and the same is true of its parents and so on. Working back through a number of generations, the number of ancestors doubles with each generation, and very soon we come to numbers that are very much higher than the number of animals or birds in the species.

For this reason, it is practically impossible for two animals belonging to one group to be unrelated. One method of measuring the intensity of in-breeding is according to the number of actual ancestors compared with the theoretical number of four grandparents, eight great-grandparents and so on. We can speak of the "loss of ancestors" in the sense of the German authors on the subject. For our present purpose this method will suffice to give us a general idea about in-breeding. The most intensive system of in-breeding is the repeated mating of a brother with his full sister. In the ancestry of every animal in such a line there are only two grandparents, instead of four, only two great-grandparents instead of eight, and only two ancestors in every generation further back, instead of the

theoretically possible 16, 32, 64, 128 and so on. In plants, self-fertilization still more rapidly reduces the number of ancestors, but none of the domestic animals are self-fertilized.

In some of the habitually self-fertilized plants, this strict in-breeding has gone on from immemorial times; in animals the best examples of strict in-breeding are found in the laboratory animals. Drosophila have been in-bred, full brother with full sister for hundreds of generations in some series. But even in the higher animals we have examples of mice and rats and guinea-pigs being in-bred, brother with sister, for several dozens of generations.

Strict in-breeding differs from random mating especially in that an in-bred line is isolated from the rest of the population. In an in-bred line we are, genetically speaking, concerned only with the variability that exists within this isolated group, and with the inherited factors present in the material and not with factors present in other groups.

If we take the number of factors for which all the animals of the group are not alike and homozygous for our measure of genetic variability, the total potential variability, we must see that only mutation can heighten this potential variability.

It is a well-known fact that in-breeding quickly lowers the potential variability of a group. Why should this be so? If we start in-breeding with one pair of animals, this one pair may be heterozygous in regard to a number of genes. One of the two may be *AA*, the other *aa*; one may be *AA*, the other *Aa*. Both may be heterozygous for *A* (*Aa*), or one may be heterozygous *Aa*, and the other one *aa*. In all those cases, young of different hereditary make-up are born from such parents. If in our calculations we reckon with a progeny of twenty young from each mating, with all those young again breeding, it is clear that such a group can never lose its original potential variability. Why, then, should in-breeding generally lower the potential variability of a group?

The fact is that in reality a group in which only brothers and full sisters mate together could not go on expanding indefinitely. Moreover, we are not concerned with such a group within which strict in-breeding is the rule considered as a whole, but we are concerned with the separate isolated lines in such a group. For in such a group at any generation a number of parallel lines of descent exist, which have no lateral connexions.

In considering what happens to the potential variability in an in-bred line, we must compare each mated pair with the one pair of parents they share and with one of the pairs of offspring that will procreate. If we do this, we see that wherever a pair of animals are not both homozygous for one particular gene there is a chance that a pair of their offspring will be alike and homozygous in respect to that gene. Every time this happens the potential variability will drop one point. A few examples:

A pair, consisting of two heterozygotes for *A* (*Aa* and *Aa*) will have 25 per cent. *AA*, 50 per cent. *Aa* and 25 per cent. *aa* offspring. The possible pairs of animals in this generation will be:

I	*AA* and *AA*: One chance in sixteen
II	*AA* and *Aa*: Four chances " "
III	*AA* and *aa*: Two chances " "
IV	*Aa* and *Aa*: Four chances " "
V	*Aa* and *aa*: Four chances " "
VI	*aa* and *aa*: One chance " "

Even if both parents of a pair of young are heterozygous (*Aa*) the chance is one in eight that the new pair will consist of two homozygotes, either both *AA* or both *aa*. This means that even if both parents are heterozygous, the potential variability is divided by eight in one generation. When one parent is homozygous, the other heterozygous ($AA + Aa$ or $aa + Aa$), the chance that the pair of the next generation will consist of two homozygotes will be one in four. Only when one parent is *AA*, the other *aa*, the potential variability in regard to that one gene will be kept at its former level during that one generation.

This means that if we start from one pair of animals and continue in-breeding by mating a full sister with a full brother in every generation, the potential variability of this group will steadily diminish automatically.

In regard to every factor for which the members of any pair are not alike and not both homozygous, the chance is about one in five to six that the next pair will be homozygous. This means that in six to ten generations of continued in-breeding of brother with full sister, the line must be practically pure for all the genes present in the stock, unless mutations have been very frequent.

Where the in-breeding is not as strict as all this, but where a herd is closed to cross-breeding with animals outside it and matings within the herd are random, the potential variability

still diminishes. The smaller the herd, the more intense is this falling of the potential variability. Lush, in his *Animal Breeding Plans*, gives a very useful formula. The reduction of the potential variability in such a population is just a little smaller than $\frac{1}{8M} + \frac{1}{8F}$; here M is the number of males, and F is the number of females that have adult descendants in each generation. In a group where three males and six females exist, this would come to $\frac{1}{24} + \frac{1}{48}$, or one-sixteenth. It can be seen that reducing the number of males in a breed (see the chapter on artificial insemination) helps to reduce the impurity in a breed of animals. In a group where in every generation there is only one male to six females, the reduction of the remaining potential variability would be $\frac{1}{8} + \frac{1}{48}$ or about one-seventh.

We have seen that in-breeding reduces the potential variability of a group; but we know that, paradoxical as it may appear, in-breeding heightens the apparent variability. To explain this we must remember that in a population in which the majority of animals are homozygous, *AA*, a few heterozygotes may exist (*Aa*). Where the mating is wholly at random and where no difference is discernible between these heterozygotes and the homozygotes, almost always such heterozygotes will mate with homozygotes. From such matings 50 per cent. of the offspring will be again heterozygous, but in every generation the chance of two heterozygotes mating together is relatively small. When in the population one individual only out of every n is heterozygous, the chance that two heterozygotes will happen to mate together is one to n squared ($1/n^2$). This means that if 1 per cent. of the population is heterozygous, only one mating in ten thousand will be between two heterozygotes.

When, however, in-breeding occurs, everything changes. A heterozygote, when mated to a homozygote, will produce 50 per cent. heterozygotes. When we mate a brother with his full sister, it may happen that one of the parents of this pair is heterozygous, and if this is so there is one chance in four (25 per cent. chance) that our pair consists of two heterozygotes, and will therefore produce some young lacking the factor in question.

When no matings between full sisters and brothers are made, but only between first cousins, the common grandparent of such a pair may be heterozygous, and in such a case it is possible that each of the two mates has a heterozygous parent and is

itself heterozygous. Everybody can easily calculate how big the chances are that recesssives are born in cases where either full sibs or first cousins are mated, given the frequency of heterozygotes in a population.

In-breeding greatly enhances the possibility of the mating of heterozygotes and thus the production of recessives. In our domestic animals many animals are heterozygous for important genetic factors. For this reason in-breeding in almost any stock will produce a certain proportion of worthless offspring.

What is known as "degeneration" caused by in-breeding is nothing else but this phenomenon. Experiments with many animals and plants have shown conclusively that degeneration after in-breeding is really caused by a hidden potential variability, heterozygosity of the material. This is clearly illustrated by the fact that long-continued in-breeding makes a group resistant to the degenerating effect of in-breeding, "in-breeding-resistant". Plants such as wheat, peas, beans, where self-fertilization is the rule, are very resistant. All of us who breed mice and rats for experimental purposes have our in-breeding-resistant stocks, in-bred, brother with sister, for ten to eighty generations. In such families of mice, no bad effects of in-breeding are ever noticed; but this does not mean that mice in general are in-breeding-resistant. On the contrary, when one starts to in-breed mice, all sorts of undesirable, unthrifty, infertile and unhealthy individuals are almost sure to crop up in the first generations.

It is very probable that many breeds of domestic animals are practically immune to bad effects of in-breeding—they have been in-bred so intensively that they are very pure. I am thinking of the white-crested Poland fowl and of the Black Lahore pigeon, and similar breeds.

The bad effects of in-breeding, being due to heterozygosity of the stock, are mainly due to cross-breeding in earlier generations. This is one of the paradoxes we meet in this subject. In-breeding produces variability and the production of undesirable individuals, but the only remedy is not out-crossing, which lays the foundation for much more impurity, but more and long-continued in-breeding.

In my long co-operation with animal breeders of different kinds one thing stands out prominently, as far as in-breeding and its results are concerned: there is a very close connexion

between the value put upon different qualities of the animals by the breeders, and the qualities in respect to which degeneration is noticed. When a group of breeders are using in-breeding as a means of purifying a breed which they value chiefly for one certain quality, the breed will always improve in respect to that same quality, and no degeneration in this respect will ever be noticed. If any degeneration occurs, it is always in respect of some quality that has been neglected. A few examples will make this clearer.

In the white-crested Polish fowl the breeders are always trying to improve the size and the shape of the topknot and the length of the feathers. In-breeding has been very common in this breed. The breeders have always used their most outstanding birds for breeding, and have not been concerned very much with fertility. If a hen laid only a few eggs, they would not think of scrapping her for this reason. One of the results has been that the breed has greatly "degenerated" in respect to egg production.

In egg-laying breeds of poultry, such as the Light Sussex and the Rhode Island Red, some of the very best-laying strains have sadly "degenerated", as far as colour and show-characters are concerned; but in the meantime the fertility has been greatly improved.

It is the great drawback of selecting animals for a few special qualities instead of for all-round excellence which causes the "degeneration" in respect to neglected points that we see in so many breeds. In real show-breeds we often meet with this sort of thing, but even the selection of animals with an eye to production can lead to degeneration on other points, when the selection is too one-sided. Here lies the danger of laying-tests for poultry, selection of dairy cows for yield alone, etc.

In-breeding is the only means of getting pure-breeding groups. The breeders, however, should realize that the purity that is the result of in-breeding is due to the system of mating related animals, whereas selection only gives direction to this process. While the group becomes pure, it does not only become pure in respect to the characters valued but all along the line. For this reason it is extremely risky to leave some of the qualities of one's animals to the future and concentrate one's energy upon the selection of the characters that appear to be the most important.

It is not true that our important breeds of domestic animals are plastic, and capable of being changed by selection. This is only true in so far as some potential variability (impurity) still remains in them, and it should be the aim of the breeders of all economically important breeds, to reduce this potential variability as much as possible. When, during the process of selection, a breed becomes fixed for a genotype of its own, it becomes less plastic and more and more fixed, and when this has happened, only cross-breeding would help in bringing back the desired variability necessary to improve some quality which had become fixed as a result of in-breeding while our attention was given to some more obviously important quality.

Just as we should give enough attention to all the possibly important qualities of any breed, we should especially avoid giving too much attention to really irrelevant qualities. If we give our attention to such unimportant things as colour-markings, shape of the backline, or set of the tail, we only make selection for really valuable qualities more difficult, as we restrict our choice to only part of the really best animals in our herds.

In our most important animals, it is necessary to use in-breeding with great caution. The best thing we can do is to select our male breeding-stock with scrupulous care, according to the quality of their offspring. In-breeding sires with their own daughters greatly helps to recognize those sires which are impure (heterozygous) for factors which we want all our animals to have, and it gives us a chance to eliminate such sires together with all their get. As soon as we come to know a few very good sires which have such a make-up that all their offspring are valuable, we must employ these sires as far as possible to the exclusion of less valuable or even of untried young sires. Artificial insemination may be of very great help in doing this.

The use of in-breeding in selection makes it necessary to avoid the use of any but the very best breeding stock available. No one should ever be led to use faulty animals in an in-breeding programme. Most faults are recessive, and it is obvious that if in a certain generation all animals are *aa* it is never possible to get factor *A* back into the group without cross-breeding.

It is easy when in-breeding to get certain faults fixed in the group, because the material becomes homozygous for genes affecting the quality. Just as it is impossible to get animals

having A when in a certain generation all the members of an in-bred group have the constitution aa the reverse is true: when all the individuals in the group are homozygous for a factor A (AA) no amount of selection can get rid of A—all individuals and all germ-cells will have it.

Breeders should never start in-breeding with a group of animals in which the best ones are not yet quite as good as they would like to see them. When in a variable group some animals are excellent, good enough for the purpose for which we keep them, then it is often possible to use in-breeding to great advantage with the object of making the majority of the animals pure for the inherited make-up of the exceptionally good foundation stock.

The idea of starting in-breeding with a group of animals of mediocre quality, with the idea of selecting them and improving their quality, should never be entertained. As long as the best animals in a breed are not yet quite as we want them, crossing within the breed or even cross-breeding with individuals of related breeds should be resorted to, until enough excellent individuals are produced to furnish us with high-grade foundation stock with which to start in-breeding.

The object of out-crossing is often to produce the necessary variability. Sometimes we want to add to the group one or two genetic factors that have been either lost inadvertently, or that have never been part of the make-up of the group. At another time we want to make it possible to remove one or more factors in regard to which all our present animals are homozygous.

Out-crossing must always be considered as an evil, sometimes an unavoidable evil, but to be avoided wherever possible. The object of animal breeding is almost always to purify a group of animals for the inherited make-up of the very best individuals of the group, and out-crossing destroys purity. When it is unavoidable to employ an out-cross, we always get very much more than we need in the way of genes foreign to our breed or strain. We may obtain the factor we want, but in addition we also obtain a number of factors we certainly do not want, and after each out-cross the slow process of weeding out undesirable individuals will have to start all over again.

Very often the immediate effect of an out-cross is excellent. Two strains of animals of the same breed may "click" very well, so that the animals of the first cross, considered as individuals,

are excellent. This is often the fact when the reason for the out-cross is the reinstatement of a gene that has been lost from the group. But even where the first-generation animals are excellent in themselves, their potential variability is very high, and much of the painstaking work of purifying the strain by means of in-breeding must be done over again.

Where an out-cross is considered necessary it is wise to keep in mind the dangers incurred by out-crossing, and to do the work in such a way that the good work done before is not all undone by the out-cross. The first rule in out-crossing is to confine the effects of the cross to a small portion of the group affected by it. The object of the out-cross being the addition of one or two genes to the make-up of the group, we should try to get rid of all the undesirable new things introduced into the first-generation animals while holding on to the necessary gene. This can be done in the way indicated in the chapter on adding a gene. The hybrids must be bred back to pure-bred animals of the strain, and from the progeny of such a mating only a few individuals should be kept, namely, those showing the improvement most markedly. Again, those few animals should be bred to pure-bred individuals of the strain, and so on for at least three to five generations, but longer if possible. With the exception of the few animals needed in the work, the animals produced by the repeated back-erosses should be thrown out of the pure group, no matter how good their individual quality may be.

The most common breeder's mistake is to use an out-cross unwisely. If the first crosses are excellent, many breeders make the mistake of using them for breeding in the group in an indiscriminate way. This should always be avoided. In polygamous animals, no males, derived from an out-cross should be used during at least four generations; the added genes should be introduced through the female lines where the added impurity can do less harm.

Where shall a breeder go for an out-cross? The answer must depend upon circumstances. It will always be best to stay in the breed, if a strain can be found which is superior in the point that needs improvement. If necessary, a cross between different breeds must be made, but if this is done very great care is necessary to minimize the dangers of introducing all sorts of uncalled-for impurities. A careful breeder who understands

genetic principles and can figure out what really happens, so that he is very careful not to use impure animals indiscriminately, can do excellent work in this way, but such work should not be lightly undertaken.

Everything I have been saying on the subject of out-crossing has been meant as a warning to breeders who want to purify and ameliorate strains of economically useful animals: in such stock individual quality of a few superior animals is never worth as much as the average good quality of large groups.

The advantage of what is sometimes called line-breeding lies in the fact that parallel in-bred lines need not develop wholly in the same way. When two or three parallel in-bred lines are maintained, the breeder has a guarantee against the involuntary loss of valuable genes by in-breeding. It is possible that in one line a gene is dropped, so that in one given point the animals are seen to be inferior. It is then very fortunate if another parallel in-bred line exists in which this same mishap did not occur; an out-cross with an animal of the other line is then indicated. If the two lines have not been separated too long, it is highly possible that not very much impurity results from such an out-cross with a related in-bred line. Line-breeding, looked at in this way, is a method of retaining the possibility of re-instating genes that happen to get lost during in-breeding. A breeder who establishes three or four parallel in-bred lines instead of putting all his eggs into one basket does not need to take all those precautions a man with only one line must necessarily take.

The best method of in-breeding modified into line-breeding is a system in which two or three breeders start in-breeding in the same breed, as far as possible with animals of the same source. In such a scheme it is possible for each of those breeders to use a few animals of his colleague's stock for an out-cross when such a thing happens to be necessary.

There is always some danger when a breeder begins breeding-in that he gets discouraged by the production of many inferior individuals in the second or third generation. In the first generations the quality of the stock, measured as an average of everything born, may be below par. The thing to watch, however, in in-breeding during the first three or four generations is not the average quality but the quality of the best individuals, which must be used as breeding stock. During the

first generations it will be necessary to discard a great number of animals, for it is really a matter of purifying the breed of unwanted material.

Whereas in economically valuable animals purity is the main thing aimed at after quality, the same is not true in show stock. After an out-cross the variability induced is a great disadvantage in economically useful animals. The same thing is not true when we are breeding animals for show purposes; here the object is not the group but the individual; purity is no great advantage. Again, the standard of excellence is not fixed by economic usefulness; the judges simply follow the fashion, and fashions in show animals change in just the same way as fashions in ladies' dresses.

In breeding dogs or bulls or canaries for the shows, an out-cross, even a rather wide out-cross, may furnish the variability that makes it possible to produce an animal with some fashionable point exaggerated to such an extent that it catches the eye of the judges.

The purification of breeds by in-breeding defeats its own ends when the breeding of show animals is concerned, for as soon as some quality is fixed in the breed it may become outmoded.

The worst possible conditions are met with in those instances in which really valuable animals, that are used economically, are also exhibited at the shows. Whereas the users of the breed want uniformity for a high level of quality, the show-breeders want to produce a few topnotchers for the shows.

When the craze for cattle shows began in Holland, Shorthorns were imported from England to "improve" the type of the Black-and-White cattle of the Netherlands for show purposes, and the result has been that ever afterwards at the shows, the Dutch cattle are considered as a "dual-purpose" breed, and are judged accordingly, whereas the real cattle farmers employ the breed as a milking breed, just as the Americans do who imported their best Dutch cattle before the craze for Shorthorn type arose in Holland. This out-cross must have done more harm to the excellent milk-breed than many epidemics; it has destroyed much of the former uniformity, and the breeders in Holland are even now striving to eradicate the last traces of impurity due to the cross.

NOTES

"In-breeding is the only means of getting pure-breeding groups."

This categorical statement of Hagedoorn's is manifestly true. Without a certain degree of in-breeding there can be no measure of pure breeding. Indeed, it seems fair to say that the basic distinction between pure-bred, pedigreed livestock and what is somewhat loosely called "commercial", unpedigreed livestock lies in the closer degree of in-breeding associated with the former class. It is, of course, a mere assumption, often contradicted in practical experience, that pure-bred livestock are either the more economic or the more productive. They are, however, indubitably more uniform in appearance if not always in performance. Thus the distinction between breeds is only possible through a measure of in-breeding of variable degree. It was by imitation of Bakewell's method of in-breeding that the modern breeds of livestock were first formed.

Theoretically, in-breeding carried to its ultimate limit of the repeated mating of full brothers and sisters should lead eventually to complete uniformity both in appearance and in performance provided environmental conditions were also kept entirely uniform. There would result what might be considered for practical purposes as a population of identical twins. Such completely in-bred and uniform populations have in fact been established in several species of laboratory animals. That, however, is by no means the case with farm livestock.

Genetically speaking, none *of our breeds of farm livestock are pure or homozygous, although the term "pure-bred" is customarily applied to them. The breeder of "pure-bred" farm livestock when, as he must do, he indulges in an in-breeding policy does so cautiously, hesitatingly, one might say almost fearfully, and he always stops half-way or quarter-way. The reason is the degeneration or apparent degeneration which almost always follows upon the commencement of a policy of close in-breeding. The genetic interpretation adopted by Hagedoorn—and it is a plausible one—is that in-breeding leads to a segregating out of recessive characters, mainly undesirable characters, through the mating of individuals heterozygous for the same recessive gene. Adopting this interpretation, close in-breeding might be regarded as a method of breed purification. There is always the possibility, however, that if there were too many impurities segregating out, there might be no breed left to purify.*

To avoid, or at least to minimize, the consequences of such "degeneration" so liable to follow upon any policy of close in-breeding, the practical breeder of livestock has adopted certain breeding techniques. Perhaps the most common is the "mild out-cross" in which a period of in-breeding, say by the use of a series of home-bred sires, is interrupted by the use of a bought-in sire from another herd or flock of the same breed.

Another technique, frequently employed, is that called "line-breeding", a term which may be used in at least two different senses.

One type is simply a modified form of in-breeding in which the mating of close relatives, such as full brother to full sister, sire to daughter or son to dam, is deliberately avoided. Very frequently the line-breeding policy is designed to hold the breeding contribution of some admired ancestor in the herd or flock for as long as possible. "Line-breeding" may in this case consist in breeding back *to one particular ancestor, and it is in that sense Lush uses the term.*

Another meaning of the term "line-breeding" is where several rather closely in-bred lines are maintained, as it were, running parallel together, within the same flock or herd. Mild out-crosses between these lines are arranged from time to time according to the judgment of the breeder.

In both cases, the breeder is indulging in what might be termed a game of see-saw, tipping the plank down first upon the side of in-breeding and then bringing it back by some type of out-cross. He steers, as it were, a difficult and somewhat hesitating course between the Scylla of breed uniformity and the Charybdis of breed degeneration. Why does he not bring the plank down firmly on the side of in-breeding?

One reason, which Hagedoorn makes abundantly plain, is that one of the first results of in-breeding is the segregating out, the unmasking of undesirable hereditary characters latent in the breed. Almost certainly a proportion of the resulting stock will be economically useless. Apart altogether from economic loss there may be, especially in slowly-reproducing species such as cattle, an insufficient number of stock of sound character left to perpetuate the breed. That could happen.

Yet it need not necessarily be so. There are too many proved instances of successful and long continued in-breeding of the closest type among several species of laboratory animals. Might not the same be true of farm animals? Once the period of apparent "degeneration" due to in-breeding was over, might not more uniform, more genetically sound stock be the expected result? Theoretically there seems no good reason why it should not, although it must be added that the rather small number of experiments designed to test the matter out have been far from encouraging.

There is, moreover, another point perhaps insufficiently recognized in relation to close in-breeding of farm animals. As already stated, there are strains among laboratory animals which have proved completely resistant to close in-breeding. There are, however, many other strains that have not. These in-breeding-resistant strains of laboratory animal—the Wistar white rat is a notable example—have served a very useful purpose in providing uniform genetic material for nutritional, bacteriological and other types of research. That, however, is not the fundamental function of farm livestock. There, a policy of close in-breeding pushed to its ultimate conclusion might result merely in strains completely resistant to in-breeding but at the same time economically useless.

The productivity rather than the homozygosity of farm livestock is the point of cardinal importance. It might be argued that the known facts suggest that homozygosity and productivity may be opposed. The weight now given to the

phenomenon of "hybrid vigour" in theory; the prevalence of cross-breeding in practice, could be interpreted very simply on the hypothesis that even the relatively mild degree of in-breeding so far indulged in has led to a certain measure of loss of productivity which cross-breeding serves to restore. In other words, hybrid vigour on such a hypothesis would be merely a restoration of something already lost, rather than an addition to something previously gained.

Chapter Twenty

Uniformity and Purity

In almost any group of domestic animals uniformity is of very great value. This is especially true of all animals and birds that have to be used in groups. It is much easier to get maximum profit from a group of animals that react in the same way under the same influences than to have to work with a lot of animals that have individual idiosyncrasies and have to be fed and treated in different ways.

In a group of pullets we want all the birds to start laying at the same time, so that we can modify the food according to production. To get this we want birds that all take the same time to grow up from the egg, so that if they are hatched at one time, production will start in all the animals simultaneously. Variability in any breed of animals is always uneconomic, we want all the animals of one group to be alike in every respect.

This does not mean that it would be enough to have one breed of domestic animals in every group; on the contrary, in every species of domestic animals we want a number of different breeds, so that we can for special circumstances use the one that is best adapted to our purpose. Within each of those breeds, however, we do not want variability, we want every animal to be like the best few we now possess.

There are different ways of attaining this ideal, and we can especially distinguish between two fundamentally different methods, namely selection in every generation of animals that suit our purpose, and breeding methods that tend to make the breed less variable and to make the future generations more nearly like our ideal.

It is clear that in every variable breed we can collect a relatively small group of animals that are, at least superficially,

alike. This is done in buying a group of horses for a cavalry regiment, when the committee has all the horses in the country to choose from. We do the same thing when we conduct a herd-book on a selective basis. When we admire the different breeds of cattle at our largest shows, we are struck by the uniformity within each breed—but this uniformity does not prove that the breed of which these animals are choice specimens is pure, or even very uniform. When discussing the influence of the shows on any breed, we must always bear in mind that the group of animals shown, or the group chosen to be registered in the herd-book, is selected because of its conformation to a preconceived type, but there does not have to be a very great amount of purity for this particular type in the breed.

It is often easy to show, by means of photographs, that the animals of a certain breed we meet at the shows nowadays are very different from the representatives of the same breed we used to get at the shows twenty or fifty years ago. If we compare those animals in the old pictures to our present show stock, we see an enormous "improvement".

Sometimes this change may be due to a corresponding change in the average quality of the animals in the breed, so that we can truthfully say that the breed has changed considerably. It is evident, however, that in some cases we are simply dealing with a changed fashion in the breed, so that we now prefer animals of one type, whereas formerly we preferred another type. It is also possible that in some of those instances, both kinds of animals are still being born continually. When a fashion changes we need not wait until the breed is changed by selection, all we need to do is to hunt up the animals that most nearly conform to the fashionable type.

When the double-laced Barnevelder was at the height of its glory as a show bird in Holland I once asked our most successful fancier how he succeeded in getting so many perfect hens together, all of one type and true to the desired feather-markings. His answer was very simple. He told me that the most economic way of getting together a good collection of show birds was to visit a great number of farms around Barneveld with a basket on a bicycle, with an eye to buying perfectly marked birds! Not only could we see an enormous contrast between the striking uniformity of the group of Barnevelders at a poultry show, and the great variability in the birds of that breed at the farms,

but such an inspection makes it evident that should the fashion change it would be as easy to bring a uniform collection of hens of quite a different type to the poultry shows. The point is that the uniformity we admire at the show does not prove anything about the uniformity or variability of the breed, but it is produced by choosing a few similar birds from a multitude.

If at the time of registration of animals in a herd-book we practise a certain selection, so that we take only those individuals that conform to a certain preconceived ideal and reject the others, this measure will also produce uniformity in the group of registered animals. It is clear that this is the same sort of method as that which produces uniformity at the shows. The object of this measure may be to produce a greater uniformity in the breed, and in general the real object of the selective registration is to influence the quality of the breed and to make it conform more and more to the ideal. Whereas, however, it is obvious that selective registration makes the registered group uniform, it does not follow that this selective registration greatly helps to make the breed more nearly uniform.

As long as we thought that the qualities of an animal as such were passed on to the offspring, it seemed obvious that selective registration, the selection of valuable animals and their segregation from the rest of the breed, would inevitably help to make this registered group more nearly ideal—a group of valuable animals should produce better offspring than the rest of the variable breed.

Nowadays we know that only genes are passed on from parent to offspring, so that an ideal animal can only pass on his valuable genes to his children. Evidently, however, part of his quality depends upon non-inherited developmental factors, upon favourable environment—and those factors are not passed on to the offspring.

In some of the continental European cattle herd-books, no animal can be registered that does not score a certain number of points. Those points are given according to beauty in respect to definite show points, so many points for horns, so many points for back, so many for set of tail, etc. The result is that a group of registered animals in those countries does not contain any animals that do not conform to the preconceived standard of beauty of the moment.

At first sight it seems logical that those qualities are highly

hereditary, that they are chosen because the breeders know that there is a strong correlation between quality of parents and offspring as far as those points are concerned. In other words it seems probable that an animal that scores highly for some special quality will produce offspring that are better in this respect than the common herd. Recent investigations in Holland, however, have shown the surprising fact that this is not necessarily true. The correlation between quality of a father and quality of the offspring in those points is insignificant. It is by no means true that a bull with an exceptionally beautiful back will produce daughters with better points for back than the daughters of a bull that personally scores very low on this point.

It is certainly true that particular bulls produce daughters that average very high in certain of these respects, but those bulls themselves are not necessarily very good in the same respect. This can only mean, that selective registration is grossly overrated as a method of producing uniformity *in the breed.* It certainly produces uniformity *in the registered group,* but this is something altogether different.

The ultimate goal of breeding a group of animals is to make the group so pure that every animal will react in the same way to the same environment. Genetically speaking, a group of animals is absolutely pure when all the animals of one sex have the same inherited make-up, and are pure (homozygous) for all those genes for which homozygosis is possible in a group with two sexes.

We never know absolutely how much genetic variability is present in a group of animals, but we do know that after all the number of genes for which not all animals are alike and homozygous is a definite one. I have introduced the term "total potential variability" for this number of genes, in respect to which the animals of a group are not all homozygous. Working towards purity in a breed of animals means trying to reduce the potential variability, or in other words to reduce heterozygosis.

In a group of animals in which there is no preferential mating and no difference in fertility, the total potential variability remains the same: but it is certain that in no breed of domestic animals are those conditions fulfilled. When from generation to generation the number of animals in a given group remains unchanged, this could be said to mean that every animal in one

generation on the average produces one animal in the next generation. Even if this is true in a mathematical sense, it does not mean that all animals, or even that most animals in the group, produce just one descendant each. In reality a few animals have many children, and a great many do not reproduce at all: and the exclusion of a great number of animals from reproduction reduces the potential variability of the group.

When a certain gene is very rare in a group of animals, so that only a few animals carry it, it depends upon chance whether such animals will or will not reproduce many offspring, and for this reason the proportion of animals in a breed which carry one of these rare genes fluctuates enormously. It is possible that, from a certain moment on, the rare gene disappears from the group because the animals carrying it did not happen to produce any offspring.

Another cause of reduction of variability is isolation. When a group of animals is isolated from random mating with the rest of the breed, the isolated group will necessarily have a potential variability, which is below that of the breed as a whole. Even when we divide a breed into two equally large parts, each of the two new groups will have a lower potential variability than the original group, because rare genes are not equally distributed over the whole area covered by the breed, and the same is true of rare impurities (heterozygosis for genes for which almost all the animals are homozygous).

The fewer the animals that take part in reproducing the breed, the quicker will the potential variability be reduced. For this reason reduction of variability, and therefore automatic purification of the breeds, is much quicker in swine than in horses or cattle.

In the polygamy of our domestic animals we have the means of reducing the potential variability of our breeds. The fewer males we use, the stricter can we select those few. By methods of artificial insemination we can greatly cut down the number of males we need to use in every generation, and if we see to it that those few males used have been selected in such a way that we know them to be homozygous for the most important genes in the breed, we can purify the breed very effectually.

When we want to produce pure breeds of animals we must eschew everything that raises the variability in our groups. This means that it is worth while to make some sort of a census

of the different breeds of animals in any country, and to ensure that no two groups are ever amalgamated. Where local breeds exist, we must keep them apart as much as possible, and try to make them as pure as possible. Where necessary we can change over a group of animals of one sub-breed into a different sub-breed by a process of deliberate grading over, by using males of breed A to cross with females of breed B and their female progeny, in order to change breed B into breed A in a few generations. Apart from this we must try to keep the breeds and sub-breeds free from inter-crossing.

When a group of animals is inter-bred continually, the potential variability automatically diminishes. A system of selection will give direction to this process.

The smaller the number of animals breeding in any generation in relation to the total number present, the quicker the potential variability is reduced. This is the reason why in-breeding produces purity. This is most easily explained by comparing the strictest in-breeding, continued mating of a full brother with a full sister, with random mating within the group. Let us consider one particular gene, *A*, for which the breed is not pure. This means that there will be a certain number of homozygotes of two kinds, *AA* and *aa*, and also some heterozygotes, *Aa*. When we start a series of in-breeding generations, we may start from one pair. Such a pair may consist of two *AA*'s or of two *aa*'s, but it may also consist of one *AA* and one *aa*, or of an *AA* and *Aa*, or *Aa* and *aa*, or even of two heterozygotes, both *Aa*. In pairs consisting of two *AA*'s or two *aa*'s, no further variability due to presence or absence of *A* will be found in subsequent generations. A pair consisting of one *AA* and one *aa* individual will give only heterozygotes, *Aa*. All the other combinations will produce some homozygotes, either *AA* or *aa* or both. A mating of two heterozygotes (*Aa*) together will give 50 per cent. homozygotes, so that the chance that the next generation will consist of two similar homozygotes (*AA*'s or *aa*'s) will be one in four. We can calculate all the chances in all the possible combinations, and if we do this we see that it takes only few generations of brother-sister matings to get rid of heterozygosis for any gene.

NOTES

"In its preoccupation with purity as a panacea, the book is perhaps most out of touch with recent genetic thought."

This sentence, taken from Wiener's review of the 5th Edition of Hagedoorn's book (A.B.A. 1955, 23, 958) may or may not be justified, but certainly if Hagedoorn over-emphasized the importance of purity in livestock breeding, he is not alone in doing so. His error, if it be error, is shared by every Association or Society sponsoring any particular breed. It is one of the features of this chapter that Hagedoorn shows so clearly and convincingly how Breed Societies are failing to achieve that aim. Thus, Hagedoorn wrote:

"There are different ways of attaining this ideal, and we can distinguish between two fundamentally different methods, namely selection in every generation of animals that suit our purpose, and breeding methods that tend to make the breed less variable and to make the future generations more nearly like our ideal."

Although the intention of Breed Societies is to make their breeds less variable by breeding methods, it is, in fact, as Hagedoorn emphasized, very largely by selection in each succeeding generation of animals that a somewhat illusory measure of uniformity is actually obtained. The method of selective registration so widely adopted gives an impression of breed uniformity or purity that is rather misleading. As Hagedoorn wrote:

". . . selective registration is grossly over-rated as a method of producing uniformity in the breed. *It certainly produces uniformity* in the registered group, *but this is something altogether different."*

Still more is the apparent uniformity of any breed in the show-yard due to careful selection rather than to uniform breeding, for unless an individual of any breed corresponds to accepted breed standards it will never be shown.

The fact that Breed Societies and Associations in general fail to hit the target they aim for does not mean necessarily, however, that the target they aim at is out of range. There may still be justification for Hagedoorn's contention that:

"The ultimate goal of breeding a group of animals is to make the group so pure that every animal will react in the same way to the same environment."

Not being a geneticist by specialization, I am inclined, perhaps, to lay less stress upon the breeding factor in animal production as compared with nutrition and husbandry than Hagedoorn would have done. Nevertheless, I am certain that uniformity of production would be an undoubted advantage and a desirable simplification in practical animal husbandry. If every cow had the same potential milk-yield, all ewes bore the same number of lambs and all meat-producing animals had the same potential growth rate appropriate to their species, it seems to me that the possibilities of labour saving and of mechanization would be vastly increased. When, therefore, it appears that Hagedoorn is "out of touch with recent genetic thought", is it fair to assume, unreservedly, that Hagedoorn was necessarily mistaken?

Chapter Twenty-One

Test-mating

In most instances the quality of a breeding sire depends upon so many different genes that it is not possible to compare a number of sires before each has produced numerous offspring. There are, however, certain cases in which one or two genes are of sufficient importance to make it worth while to find out whether a young sire is homozygous in respect to them. This is especially true where we are dealing with a gene that differentiates valuable animals or birds from individuals with obvious faults.

In general we can say that deliberate test-matings are valuable only when we want to find out whether a male that shows the presence of a valuable gene is homozygous or heterozygous for it. There are two different ways to proceed in making such test-matings. The easiest way is always the cross with the corresponding recessive. In general, where test-matings are useful, the situation is such that the majority of our animals in the breed possess a certain gene, but as a proportion of the individuals are heterozygous in respect to it chance matings of such heterozygotes together will result in the birth of a few individuals that lack the gene in question.

In almost all breeds of cattle in which the standard colour is black, occasionally a red calf is born. This happens in the Black-and-White Dutch cattle, in the Aberdeen-Angus, in the Kerry. Even in breeds where red males are always rejected a few red calves crop up continually.

One of the simplest examples in poultry is that of the single-comb culls in such rose-combed breeds as the Wyandotte. No matter if the breeders continually reject single-combed animals from the breeding-pens, single-combed chicks will

turn up in every generation in many flocks. In sheep we have a similar instance in regard to colour. In such white breeds as the Dorset and the Lincoln or the Texel occasional black lambs are born even if black animals are never used for breeding.

In all those instances, deliberate test-matings of males will help to obviate the birth of such undesirable recessives. We can use test-matings to purify the breed, or certain families within the breed, or simply to get rid of the recessives in a certain generation. Let us examine a concrete instance. A breeder of Wyandottes who sells eggs for hatching finds it to his advantage to ensure that none of the eggs he sells will produce single-comb chicks. Here the remedy is very simple. He knows that every spring he will have to use a certain number of young, untested males in his flocks. It will certainly pay him to test those males for purity before mating them to his Wyandottes. All he needs to do is to mate a few more young males than he actually needs with single-comb hens, e.g. to Leghorn hens, and to hatch a batch of chicks from each mating. When a male, mated with a Leghorn hen, has produced ten to a dozen chicks, all rose-combed, the breeder can be reasonably sure this male is pure. On the other hand, the first single-comb chick from such a test-mating shows him to be impure, and this makes it necessary to reject this cockerel as a breeder.

In testing young bulls in a black breed, or young rams in a white breed, each male must be bred to several females, because each mating only produces one or two offspring. Otherwise the principle is the same. A young untried ram which, when mated with half a dozen black ewes, has given only white lambs is almost sure never to produce a black lamb at all when mated with untried ewes.

Wherever it is possible to test-mate an animal in order to find out whether it is pure or impure in regard to an important gene by mating it to the corresponding recessive females, this is the very best and easiest way of test-mating.

Sometimes, however, the recessives are not viable. In many families of animals, heterozygosis exists for a few genes that are absolutely indispensable for normal life of the young animals, so that those young that are born without the gene must die. Obviously these are the instances in which test-matings are most necessary, but it is equally obvious that in these circumstances

we cannot resort to test-matings of suspected heterozygotes with recessives.

Here we have two different possible systems of test-mating. In the first place we can mate the males we want to test with heterozygous females. In swine, atresia coli, an inherited abnormality in which the gut ends blind, exists in certain strains. In these strains we can test young males by mating them with sows that have already produced some of these abnormal young. If a young boar after mating with such sows produces three or four litters of pigs in which the abnormality does not occur, he is almost sure to be homozygous for the required gene, so that he will never get piglets with the abnormality, no matter which sows he is mated with. In cattle, certain families exist in which bulldog calves are occasionally born. Cows that have produced such monsters are valuable, in so far as we are sure that they are heterozygous and that they can be used for testing young bulls.

The second system of test-mating males consists of in-breeding them to their own daughters. If a male is heterozygous in respect to any gene, *Aa*, one-half of his daughters must also be heterozygous, *Aa*. Therefore, if we mate him to a number of his own daughters, 25 per cent. of the offspring of half the number of his daughters must show the abnormality due to lack of a gene. If, therefore, a male when mated with his own daughters (at least six daughters) has produced twenty young in which the abnormality does not occur, he can be considered as homozygous.

This system of in-breeding of sires to their own daughters takes much more time than a direct system of test-mating with recessives, but in certain respects the system has great advantages. In test-mating young sires with recessive females, we test them for homozygosis in respect to definite genes, for which we have reason to suspect heterozygosis. If, however, we breed a sire to a number of his own daughters, we do not test for one or for two definitely known genes only, but in addition to this we test the animal in respect to all valuable genes that affect quality in our breed.

As in some animals many lethal and semi-lethal abnormalities exist, as in pigs, it is high time for breeders to learn to recognize the importance of this system of test-mating sires. It is very undesirable that some animals should become known as great sires

on the incomplete evidence furnished by selected groups of the excellent individuals among their progeny, when these same sires are known by insiders to produce aberrant individuals among their progeny.

Whenever a group of animals of a new breed is imported into some country, one of the first questions asked should be that of the genetic make-up of those animals. In such instances the evidence of test-matings should be used, and it would not be too much to require that any sire, to be eligible for importation, should have produced a stated number of young from his own daughters without producing aberrant stock.

Several instances are known in which important lethals were introduced into a new country by the importation of apparently sound breeding stock, such as Dutch Black-and-White cattle into Norway, Danish pigs into Holland, Swiss goats into Holland, etc.

So far we have spoken of test-mating only as a method of finding out the purity of individual sires. It is evident that such test-matings of males, when persisted in during several generations, help very much to rid a strain of animals of unwanted heterozygosity.

If a breeder of Wyandottes always tests all his young males and always rejects the heterozygous ones, keeping for breeding only those males that are homozygous for the gene present in rose-combed birds, this will soon bring down the proportion of heterozygotes in his strain. As every heterozygous hen (*Aa*) when bred to a homozygous male (*AA*) will give 50 per cent. homozygotes, whereas all the homozygous hens will give nothing but homozygotes when only tested homozygous males are used, the proportion of heterozygotes in the family is reduced 50 per cent. in every generation.

Let us suppose that in a family of Wyandottes one bird in ten is heterozygous for the gene in question. This would result in one mating between heterozygotes in every hundred matings per generation, and therefore in one chick being single-combed in every 400 chicks born. By using only tested homozygous males during one generation, the breeder would have no single-combed chicks at all during that generation, and the proportion of heterozygotes would go down from one in ten to one in twenty. This means that, even if he only test-mated his males during one single season and left everything to chance in

future, he would in his stock have only one mating between two heterozygotes in every 400 matings, so that in future he would not have to expect one single-combed chick in 400 as formerly, but only one in 1,600 chicks born.

One generation of test-mating sires with the rejection of those proved heterozygous for any gene helps to bring the proportion of undesirable recessives down to one-fourth of what it was before.

The smaller the proportion of males used to females in any breed, the easier it becomes to use test-mating of males as a system of reducing the proportion of undesirable individuals in the breed. In other words, the testing of a given number of males in every generation will affect a greater number of females, and for this reason will bring down the proportion of heterozygotes in the whole breed at a quicker rate. When we want to get rid of the constant production of inferior animals as quickly as possible, the ideal way is to test the breeding value of several males as well as possible, and then to use those tested males as much as possible. When we can, by artificial insemination, make the number of offspring produced by a few thoroughly tested males great enough to reject for breeding purposes all the progeny of untested or not fully tested males, our progress will be extremely rapid.

When we are testing for homozygosity in regard to one or two special genes, it is obvious that in some instances we can test females as well as males. This is especially true in those animals or birds where one female produces numerous offspring rapidly. With regard to rose-comb in Wyandottes, it would be just as easy to test a number of females as a number of males by test-mating them with Leghorns. In poultry it should be possible to test females as well as males, and so to establish a family wholly homozygous in respect to one or two important genes, and the same could be said of pigs, and possibly of sheep. Only in polygamous animals testing a few males has far more influence upon the family as a whole than testing a few females. In actual breeding practice, however, there are a few instances in which deliberate test-mating of females should be recommended. Whenever we are out to produce a wholly new breed, the animals or birds constituting the new breed in its beginning are so few in number that it would certainly pay to test the females as well as the males for homozygosity in respect to especially valuable genes.

When, however, we are dealing with existing breeds, all we really want to do by means of test-mating is to reduce the proportion of undesirable recessives; and we have seen that testing a few males and rejecting those proven to be heterozygous has such an enormous influence upon the proportion of undesirable recessives in a polygamous species that we are wise to restrict our energy to the testing of males rather than to that of females.

One of the important disadvantages of the system of deliberate test-matings in respect to one or a few important genes lies in the fact that the most important economic qualities of our animals are due to the co-operation of a great many unknown genes. It would certainly not be worth while to use deliberate test-matings for specific known genes if we believed that the result—the reduction of the proportion of undesirable recessives—was only temporary; but we know the result is permanent and astonishingly rapid. As long as we take certain precautions at the moment of introducing "fresh blood" into our strain, we can, by means of test-mating, quickly reduce the proportion of undesirable recessives to a negligible minimum.

When we are using the incest method of test-mating sires, we do much more than merely test for a few known genes. This method helps to rid the breed of little-known or of unsuspected lethals and other undesirable recessives (dog scheme).

In general breeding practice, the system of evaluating the breeding value of a sire by means of the average quality of his get includes all deliberate test-mating. The term progeny-testing, however, is generally employed for something somewhat different from deliberate test-matings in respect to a few known genes. Progeny-testing will be treated in a special chapter.

NOTES

In this chapter, Hagedoorn describes in simple genetical terms the various types of test-mating and their practical applications. One type, the mating of a sire with his own daughters, might, I think, have been given more prominence in comparison with others. The Norwegian geneticist, Wriedt, considered it as being the most rigorous test of genetical worth and advised its use as an indispensable preliminary to the wide use of any sire. Wriedt gave that advice before A.I. had been incorporated as an everyday tool in animal breeding. The same advice seems to me more urgently important at this day when there is an ambition and a possibility of no more than 200 bulls inseminating all the

dairy cows in England and Wales. The wider the use of a sire the more essential it must be to prove that he is not heterozygous for undesirable hereditary characters, particularly those of a lethal or semi-lethal nature, and test-mating by breeding him to a sufficient number of his own daughters would seem to be the surest means of doing so.

Chapter Twenty-Two

Correlation

We often see that two different qualities tend to go together, and the cause of such a correlation may be difficult to find. The easiest understood are those instances in which the correlation is causal, where one quality necessarily induces the second one.

One of the best examples is the correlation between weight and height and pulling power in horses. By letting its body fall forward against the traces, a horse exerts a pull proportional to its weight and to the length of his legs from ground to shoulder.

Another example is the correlation between body size and yield in milk cattle. By selecting for yield, a given variation in size might give us larger cows that might not be more profitable, as they would probably not give more milk per acre of pasture.

A good example is the relation between height, body-weight and thickness of legs. When, of two animals, one is twice as tall as the other, the taller one may be also twice as wide and twice as long, so that it will be $2 \times 2 \times 2 = 8$ times as heavy. If we suppose that the material of which the bones and tendons are composed is the same, the legs in the larger animal must be proportionally stronger, thicker, than in the smaller animal. To support a weight eight times heavier, they must be eight times as strong. In a slice of the leg, one inch long, we must find eight times as much material in the heavier animal as in the lighter one, and for this reason the leg must be $\sqrt{8} = 2{\cdot}83$, almost three times as thick across.

The lighter an animal, the thinner its legs, as can be seen in all sorts of animals and birds. The bantam always has shanks that are proportionately much thinner than those of a large fowl, and can be recognized from a photograph for this reason.

A cow of a small breed has thinner legs than one of a large breed; it is foolish to say that the Jersey cow has a delicate constitution, as can be seen from the thinness of her legs—indeed, if her legs were as thick in proportion to her size as in a Hereford, they would be unreasonably out of proportion physiologically! If we could breed an elephant as small as a Shetland pony, it would not look like an ordinary elephant seen through the wrong end of a telescope, but it would have legs as thin as those of a pig.

Sometimes the correlation is caused by the fact that one inherited factor acts in two different ways. In mice a gene exists which acts upon colour as well as upon the propensity to lay on fat, and yellow litter mates are very much heavier than black ones. Another gene acts upon hæmoglobin content of the blood and upon markings; in certain families the spotted mice with few white markings always have a higher blood-count than those in which the coat shows more white.

Sometimes a statistically valid correlation is not causal but accidental. If we have a heavy breed of dogs that is black, and also a second toy breed that is white, in this dog population there exists a correlation between size and colour. Such correlations, however, simply depend upon the fact that the causal factors for the characters which go together are kept together by some third cause which has nothing to do with any of the qualities. Here the correlation exists only so long as no frequent cross-breeding occurs. In a hypothetical population, consisting of large black dogs, small white ones and some mongrels, there would be a considerable statistical correlation between size and colour.

In the Californian foothills, we found that a butcher would willingly pay more for a red calf than for a black one, as a matter of principle. Here a sort of loose statistical correlation existed between colour and butchering value, simply because this was a region where black or black-and-white bulls of dairy breed were used as well as red bulls of beef breeds. Although there were occasional red "milky"-looking calves, as well as a few black "meaty"-looking youngsters, it was certainly true that fifty red calves were worth somewhat more than fifty black ones.

If we apply the term selection in a general sense, a correlation of this type can be used as an aid to selection. It is true that a

boy who goes to one of the markets in Holland and buys fifty white hens will get more eggs from those hens than if he buys fifty brown ones of which he knows equally little, simply because the white ones will probably be mostly Leghorns; but this does not mean that within one genetically related group a white hen is likely to lay more eggs than a brown one.

As a guide to selection of individuals in breeding animals or birds, such "accidental" correlations are extremely dangerous, because they fail us when we need them most.

In regions where such dairy breeds as Holsteins and Jerseys are kept, and also such beef breeds as Herefords, there is some sort of a correlation between thickness of skin and milk yield. The milking breeds have a thinner skin—we could very well say they happen to have a thinner skin than those particular beef breeds. If, therefore, we buy a nondescript mongrel heifer in the market, a thin skin is a good sign when we want her for the pail, and this would be equally true in Holland, Canada and England.

In Java, however, and in other countries where some of the Zebus have been imported, a thin skin is a bad sign if one is looking for a likely mongrel heifer to milk, simply because a thin skin is often found in animals with Ongole or Guyrat ancestry. Both in Java and in England such a correlation would be untrustworthy when we were selecting cows within a pure breed; the correlation holds only in mongrel and mixed populations and only in a general, statistical sense.

The moment we really put such correlations to the test within a pure breed they are found wanting; if people believe in them, this is never the result of experience, but almost always because of an unwarranted generalization. Somebody has observed that a thick-skinned Hereford beef cow was a poor milker, and because of this he believes that, within his own breed, there must be a correlation between thickness of skin and milk yield.

It is a curious fact that the mere belief in such a correlation is sufficient to produce "accidental" correlations. If apple breeders are convinced that thorny trees are poor producers, they will weed out all the thorny seedlings, and as a result there will be no thorny trees with good apples; but if in the beginning the apple breeders had believed thorniness was a sign of quality, they would have kept only the thorny seedlings to select from, and to-day all our good apples would be thorny.

Among our domestic animals some qualities that are in them-

selves not valuable and are certainly not related in any causal way with economically-useful qualities have a certain value as "markers". An experienced farmer who goes to market to buy cows or a few shoats will be able to buy good animals rather than poor ones by just looking at them. This does not prove that the characters he looks for are really correlated with the economic qualities he wants; it simply means that he recognizes an animal as belonging to a good family. Such a farmer is experienced only as regards the breeds he knows well; when he tries to pick the most valuable animals in a breed he does not know he is as often wrong as right.

When we compare two breeds, A and B, these breeds not only differ in economically-valuable qualities but also in dozens of other points. The genotype of the two breeds may be wholly different; in one breed almost all the animals are homozygous for a factor absent from the second breed, and vice versa. If breed A in poultry lays brown eggs and has red ears, whereas in breed B the ears are white as well as the eggs, this is simply an accidental correlation. It just happens to be so, but it does not mean that in a white-eared breed the birds with the whitest ears lay the whitest eggs!

Around 1915 the Ford automobiles had their headlights close together and the Rolls Royce had its headlights very wide apart. In a street full of cars belonging to those two makes of cars, there was a very close correlation between the distance between lamps and economic fuel consumption. The smaller the distance between headlights, the more noise and the more likelihood of finding the car to be painted black instead of claret-coloured. A man who knew nothing of automobiles going out to an automobile market with a small sum of money to buy a car would be rather likely to buy a strong, serviceable car if he looked for one with a brass band around the radiator, with a loop of wire sticking out through the radiator, and a transverse rearspring, marks of the Ford of that day. This does not mean, however, that within the Ford "breed" it would help to make a car run more cheaply if we bent the lamps two inches closer together, or that it would run more smoothly if we painted it wine-coloured. Within the breed the correlations which held in a mixed crowd of cars would be valueless.

It is certainly true that most breeds of hounds have long ears, longer ears than sheep-dogs, but selection for ear-length in a

breed of beagles or coonhounds would not improve the hunting value of the hounds.

I do not want to be understood to mean that no real causal correlation ever exists between the exterior of an animal and its physiological qualities. Very often some function of an animal will leave its visible mark. A hen in full lay is easily recognized from a non-layer, and heavy milk production in a cow can be recognized by a physical examination of the beast. This is often very useful, for instance, when we want to house and feed the laying hens separately.

The duck-farmers in Holland are continually shifting the laying ducks, so-called "wet" ducks, from among the "dry" ones, and they can do this because the laying birds have a very peculiar appearance. It would be absurd to use this criterion in ducklings before the first egg to find those that will later turn out to be good layers!

It is very important to discuss the reasons that have led to the use of correlative characters in the selection of our domestic animals, and the question whether this system of selection still has its uses.

There exist several reasons that give the breeders the idea that it is important to look for correlative characters in addition to the qualities with which we are primarily concerned. Some of the economically-important characters are of such a nature that we cannot evaluate them without elaborate tests. When the agricultural shows became of importance, it became necessary at those shows to compare the animals competing for prizes, and it was obvious that in economically-important animals and birds it would be worth while if we could place them in order of real economic merit. At the shows certain qualities became of great importance because they were taken for substitutes for real evidences of economic merit. Hence the interest in the shape and size of the udder and in the escutcheon in dairy cows, in head points and pelvic bones in laying breeds of poultry.

Very often only the animals of one sex could be really tested for economic value, and it was comfortable to believe that in judging the quality of individuals of the other sex, such qualities as shape or colour, which could be compared even in the males, were of importance as "indicators" of merit.

It was soon found that animals with identical ancestry and identical personal merit often differed considerably in breeding

value. It was small wonder that the breeders were constantly on the look-out for indications, "signs" of this mysterious inborn constitution. It became more and more usual to estimate certain characters that could be directly observed as marks of "prepotency" in breeding stock.

All this ought to have changed with a better insight into the nature of heredity, due to the discoveries in the field of genetics. When it was seen that "the inherited" was multiple and consisted of many separate genes, and when it became known that an animal homozygous for a gene transmits it to all its offspring, while a heterozygote only passes it on to one-half of its children, the nature of prepotency and the cause of other differences in breeding value became very clear to the geneticists, and later to those breeders who took the trouble to study genetics or to co-operate with the geneticists.

It is very clear nowadays that personal merit, individual quality, is no guarantee of breeding value. The experienced breeders, aided by the geneticists, are gradually substituting methods of evaluating the genotype of each animal, its inherited make-up, for the old methods of trying to guess that breeding value from its own qualities.

Now, it ought to be clear to any disinterested observer, that from the moment we defer our judgment as to the breeding value of an animal to the time when we can actually measure this breeding value from the way the animal has performed as a breeder, all those methods that were destined to help us to guess the quality of a breeder, without watching the way it actually bred, have lost very much of their importance.

The greatest importance of the progeny-test as a method of recognizing breeding stock of outstanding merit lies in the fact that this method is wholly empirical and foolproof. It is evident that when we declare that sire to be the best which has done that very thing best for which we keep him, namely the production of valuable offspring, we ought to rely wholly on this test and eliminate all other aids to selection when they are of speculative value. Such indications of probable breeding value are not only superfluous, they are positively dangerous. Such indications are either right or wrong; if they are right we do not need them, if they are wrong they vitiate our results.

One of the greatest difficulties in the way of good methods of animal breeding lies in the fact that working methods are being

changed very, very slowly, even where practical breeders and scientists agree that a radical change is indicated. I am convinced that the great advance made in matters of animal breeding in Denmark was in a very large measure due to the important circumstance that here we had an agricultural country taking up animal breeding as something new, something that was not hemmed in and permeated through and through with the tradition of muddling through for centuries. For the same reason the Dutch duck-farmers, former bankers and carpenters and fishmongers, who are engaged in an industry that has grown overnight like a toadstool, in matters of selection were ready to start correctly from the beginning, so that their methods of progeny-testing and in-breeding are twenty years in advance of those employed by the chicken farmers, bogged down as these latter men are by tradition.

In some instances in which the selection of breeding stock according to the sensible system of judging a male according to the sort of stock he sires has come in, selection is still hampered to some extent by a belief in correlative characters as of some value as indications. An example of what I mean is the present-day system of breeding pigs in Holland and Germany. In both countries, especially in Holland, the Danish method of selecting boars by the infallible system of looking at the quality of their offspring has been adopted. The system is not yet perfect, and it is true that more importance should be attached to the requirement that a really representative sample of a boar's progeny should be tested, but to a very great extent the testing of half-litters for butchering quality and economic food consumption is exemplary.

Curiously enough, however, this does not mean that the importance of exterior points, formerly believed to be correlated to economic value and breeding value, is now recognized to be slight. Boars are really judged according to the quality of their piglets as hogs, but to be admitted to the test at all the boars first must pass a rigid examination on body points. The following translation of part of the requirements refers to bad points: "Very bad faults are: a narrow or wrinkled forehead, heavy cheeks, short snout, too thin a tail, bones too fine, presence of a hair-crest along the back, etc."

The best we can say for such silliness is that we are dealing with a remnant of breeders' superstitions! The possibility re-

mains that by restricting progeny-tests to a group of males which first have been selected according to body points of speculative value, some of our points are really correlated, negatively, with quality. Breeders of pigs may cherish the superstition that heavy feet show strength in the legs, but it is quite possible that heavy bones are on the whole undesirable in a hog at butchering time. The sensible standpoint in relation to exterior points is to neglect them altogether in the sires to be tested according to the value of their progeny. If we do this work well, and if we actually point out the sires whose offspring averaged the greatest economic value by actual test, it will soon be seen what the type of the resulting animals will be. The body points of our best animals should be found as a result of tests for real economic worth; it is putting the cart before the horse to reverse the process and to start from a preconceived set of points, believed to be correlated with quality, testing the real value only in animals that first fulfil those requirements!

A system of selection based upon supposedly correlative points instead of on plain rule of thumb progeny-tests can only survive as long as the men who influence animal breeding, and have been firmly trained in the old speculative system, themselves survive. In many instances no rational methods in animal breeding can be expected before the old generation of authorities has been pensioned off and has made room for better-trained successors. In such matters as the substitution of improved methods for outmoded ones, control of animal-breeding methods by farmers' co-operatives is vastly superior to control in the hands of public servants of the paternal state.

I have often discussed the widespread belief in correlations between show points (so-called "constitution") and real economic value amongst men of the pre-Mendelian era with some of the most intelligent of these men. They always find it very hard to believe that a method in which so many eminent authorities used to believe so implicitly can really be fundamentally wrong.

For the benefit of the younger generation, for I have learned that men of the old school are mostly incapable of absorbing new truths, I think it is worth while to point out that when plant breeding was brought to a rational basis, around 1910, we geneticists had to help the plant breeders in the same sort of revolution which is just now beginning in animal breeding.

Before that time plant-breeding institutes used to have long rows of microscopes with young men trying to find correlative characters to "save time" in selecting plants for economic qualities! At that time the idea that the wheat that was best for a given county was the wheat that gave the greatest amount of profit per acre in the average year—and "hang the number of hairs at the top or the width of the leaves"—was as revolutionary and contrary to "what everybody knows", as the idea that among pigs the best individuals are those that give the best return for the money invested in their keep—and "hang the hair on their back or the thickness of their tails"—is to-day!

It is very probable that true correlations exist in our domestic animals as well as in our plants between exterior points and quality. In so far as this is true, purifying a breed of animals for the inherited make-up, which is consistent with the greatest amount of profit, will bring along some of those correlative characters.

This does not mean, however, that it is wholly safe to study the qualities in the very best breeds that we now possess as a guide to selection in breeds in the process of making. In the first place the end-result of development is due to the interrelation of very many of the genes, and a gene that has a favourable effect in one breed may be undesirable in a second breed with a somewhat different genotype. Secondly, many of the body points of a very good breed may be wholly unrelated to economic usefulness; they may either just "happen" to be so, or they may have been bred into the breed because of some such superstition as the belief in thick tails in hogs.

When the breeders of swine in Germany and Holland are taught that a thin tail in a pig is terrible, and they keep to this idea long enough, it is very probable that in the end the pigs in those countries will all have beautiful thick tails, but this does not prove that a thick tail is a sign of any economically-useful quality.

Correlations between easily observable characters and qualities that are not so easy to evaluate exist in human beings as well as in domestic animals, and a few examples may be adduced to illustrate what I have said about selection.

If we want a lifeguard for a bathing beach, we can either rely upon the fact that most professional swimmers have a wide chest and a small head, and hire the man who shows those qualities

to perfection, or else we can make the candidates show what they can do in the swimming and diving line. When we have made our choice, and when we deem it safer to look for a man who can swim, it would not be wise to refuse a swimming test to all candidates who did not have smallish heads.

When we want a soprano for the opera, we can take the fattest candidate, reasoning that there seems to be a correlation between opera singing and corpulence. Or we may select a woman because of her voice after a singing test. When once we prefer a singing test to relying upon the correlation, it would be ridiculous to refuse to let any candidate under fifteen stone show how she can sing and act.

We might extend those examples just one step further. Pianists tend to wear their hair long. Now we might have such a profound belief in the correlation between hair-length and musical ability that in judging a music teacher the first thing we would require in a good teacher would be that his locks averaged well above normal length.

When, however, we use musical ability itself in the pupils as proof of the teacher's worth, we must use this sensible test to the exclusion of the other one based upon a belief in correlation.

The real reason why we use progeny-tests to find out the breeding value of the sires we employ, is the fact that we know that it is obviously safer to use the result we want to obtain as a criterion rather than some sign which we hope indicates the probability that such a result will be obtained.

In other words, when we substitute a thoroughly reliable test for a speculative one, not only do we not need the speculative test any further, but when the slightest danger exists that adherence to the magical formula debars us from making the fullest possible use of the progress to which the reliable test is the key, we should do our best to forget the magical formula that we have tried to use to find short-cuts.

Most automobile drivers are convinced that it is safer to learn to drive well and to take out an accident insurance than to rely upon a teddy-bear mascot in the back window, or upon spitting on the steering-wheel when setting out for a drive; but they have a feeling that such magical short-cuts to safety are at least harmless. I have often heard the argument that even if looking for a thick tail in a boar or for perfect horns in a bull is perfectly absurd when we want animals profitable to use, at least such

show points do no harm. There are plenty of boars, and plenty of bulls, and it is sufficient if we find the really good ones from among the group of perfectly beautiful ones. We can have beautiful animals as well as ugly ones.

This argument, plausible as it may appear at first sight, is thoroughly unsound.

When, as in Holland and Germany, every piglet born is registered, and every hog butchered is graded, it is possible to find out the breeding powers of every boar used for breeding. When we examine the relatively few boars that have been highly commended because of the fact that their offspring have been good butchering beasts as well as good to look at, we see that a great many of them are heterozygous for genetic factors every healthy normal pig must have, that is to say that a proportion of their get are deformed, non-viable or weakly. Only a very few of the well-known boars are really perfect in such very important respects.

This simply means that the pig population is still so impure that we have to examine a very large number of boars to find a few that are perfect in every respect as sires. By restricting our selection of perfect sires to those that have the show points that are fashionable to-day we simply get too few good ones! That is, we have to take too many mediocre ones and condone their faults!

In dairy cattle the situation is very similar. By first rejecting the bulls that do not pass the judge at registration time, next the bulls whose daughters and sons do not average highly from a show standpoint, we have too few bulls left to find enough excellent ones—bulls whose daughters are first-class, strong, long-lived milkers. In Holland the situation has developed to such a ridiculous extreme that only about a dozen first-class preferent bulls are alive at one time, and the average dairy quality of the daughters of some of them is not phenomenally good.

Selection in a breed of animals kept for economic reasons should always be worked the other way round. By examining the records made by the daughters of a thousand bulls, it would be possible to find a hundred that were as good in respect to economic qualities of their daughters as the preferent bulls of to-day. If, then, we only needed eighty, we might drop twenty of the aberrantly-shaped or marked ones.

It is ridiculous to say that this would mean that the animals

would tend to become less beautiful. Critics who may believe I prefer an ugly animal to a beautiful one have probably never reflected upon the origin of standards of beauty in domestic animals.

If we except such animals as goldfish and lapdogs, but limit our discussion to cattle, horses, swine and sheep, the chief points of beauty in an animal are the points we believe go together with economic usefulness. The Germans think a pig with heavy, square legs is beautiful, because they think this denotes strength and absence of leg trouble. The Danes think fine legs are beautiful, because they think fine legs show fineness of bones, which are less valuable than pork.

Now, if in selecting swine we restricted our selection absolutely to finding those sires whose offspring graded first-class as butchered hogs, and made profitable gains for the food consumed, the result would be sure to be a breed of swine of great economic value, adapted to local methods of pasturing and feeding, and absolutely right from a butcher's standpoint. Those hogs would have legs, and those legs would be the type of leg a profitable hog should have. Instead of being obliged to *theorize* about the superiority of one sort of leg over the other, we would *know*; and we would think the legs of those ideal pigs were beautiful. Beauty, everywhere, is negative, the beautiful individual being the one that shows no blemishes of any kind, no faults. A breeder of Jerseys thinks a Friesian cow abominably ugly, and the other way round. A beautiful animal is one that shows to perfection the average norm of the best, most useful animals of her breed.

The greatest drawback of the system of putting an arbitrary set of ideals of beauty, or ideals of "constitution", above economic quality lies in the circumstance that such ideals are arbitrary.

In some instances the combination of qualities looked for may be rare, simply because those qualities do not fit together physiologically. It is obvious that this could never happen if the ideal of beauty were really formed after breeding for economic usefulness had given us a set type in the very best animals of their breed. In breeds where no cross-breeding has taken place during a long series of generations of close breeding, the ideal of beauty might even to-day tend to coincide with the appearance of an excellent animal; but this is not to be expected in such mongrel

populations as our present breeds of cattle, horses and swine.

The arbitrary standard of beauty is often really dual, there being one standard for males and one for females. This is about the worst excrescence of a superstitious belief in the plasticity of breeds of animals, the idea that a breeder can mould his animals according to his preconceived notions.

A genetically-trained breeder can understand that in one breed the genetical make-up of the males must correspond to that of the females. The enthusiastic fanciers who set up the show standards have not hampered themselves with such considerations! They not only decree that a cow shall have horns of a certain shape, an udder of a certain shape and size, and a head of a certain type, but they also decree that a bull shall have horns and head and tail of a certain definite type.

The ideal in a breed of dairy cows would be to have a standard of beauty conforming to the characters of the ideal dairy cows in that breed and to select bulls according to the qualities of their daughters exclusively, without looking at them. This would automatically make the type of the males that of the males which sired the perfect daughters. It should be obvious to any intelligent person that it is absurd to want a male to have qualities which are not those of the males in a pure breed in which the females are perfect. The American Ayrshire breeders stopped judging males.

I am not creating hypothetical bugbears, for I can point to instances in domestic animals where this state of things is fully realized, and where the breeders have found the perfect remedy! I am speaking of breeds of show poultry where double matings are necessary.

In the Silver Wyandotte, as in similar breeds, the males are always several shades whiter than the females. The shows want both males and females to have white feathers, evenly set off with a regular black border around each feather. At the shows, only such hens and only such males are sent in. In reality, the Silver Wyandotte consists of two breeds, a cock-breeding strain and a hen-producing strain. In the strain used for breeding exhibition cocks, the males are perfect, and the hens have the same genotype, which results in hens whose feather-markings are much too dark for show.

In the hen-breeding strain, the males are whitish, and are never shown, while the females of course are of show type. The

breeders of such birds, Silver Wyandotte, Brown Leghorn, Duckwing, and many other breeds of poultry have been obliged to adapt themselves in this elaborate way to the arbitrary standards of beauty. It is evident that a man who buys a trio of Silver Wyandottes at a show, and starts breeding from those birds, is crossing two different strains, and will produce a mongrel population in which in the second and third generation a perfectly-marked hen or a perfectly marked male may happen to occur among hundreds of mismarked culls!

In dairy cattle, the standard of beauty, if ever we want such a thing, should obviously be that of the perfect cow, both in bulls and cows. A bull is a necessary evil, his use being the production of daughters, and everything should favour the production of ideal cows.

The standard of beauty in dairy bulls is arbitrary, just as the standard of beauty in Silver Wyandotte cocks is arbitrary. Who knows whether it would be possible ever to breed a pure race of cattle in which both males and females conformed to the present standard of beauty (scale of points)?

It is even extremely unlikely that the characters we admire in a show bull are produced by a set of genes that, in a cow, would give a perfect animal, even from a fancier's standpoint.

This is where an arbitrary standard of points can be extremely dangerous to the breeding of utility stock. It is possible, even probable, that in restricting the selection of progeny-tested males to a group of males from which those not conforming to show standards have been rejected, we cannot possibly find the sires whose daughter-groups consist of valuable dairy cows only. It might be possible that those perfect bulls would be more abundant in a group of bulls that were of less extreme "male" type, or that had some other genotypic peculiarity, which made us reject them.

Even if in relation to bulls we are using a standard that calls for a genotype different from that which we have in standard cows, so that in breeding champion bulls to champion cows we are really crossing animals of different inherited make-up, this does not preclude the production of a few excellent bulls and a few show cows. If we persisted in mating show males in Silver Wyandottes with show females, we would also have an occasional fine male and an occasional show hen.

An arbitrary standard of show points in an economically

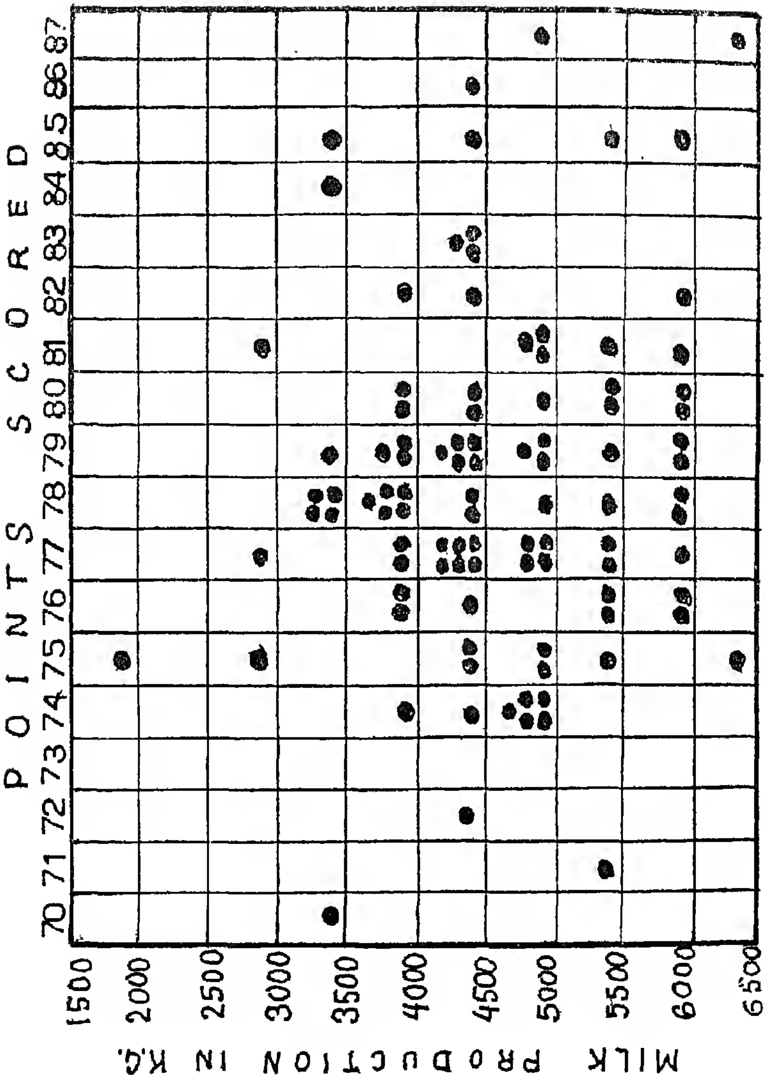

P O I N T S S C O R E D
70 71 72 73 74 75 76 77 78 79 80 81 82 83 84 85 86 87
1500 2000 2500 3000 3500 4000 4500 5000 5500 6000 6500
M I L K P R O D U C T I O N I N K.G.

TABLE IA

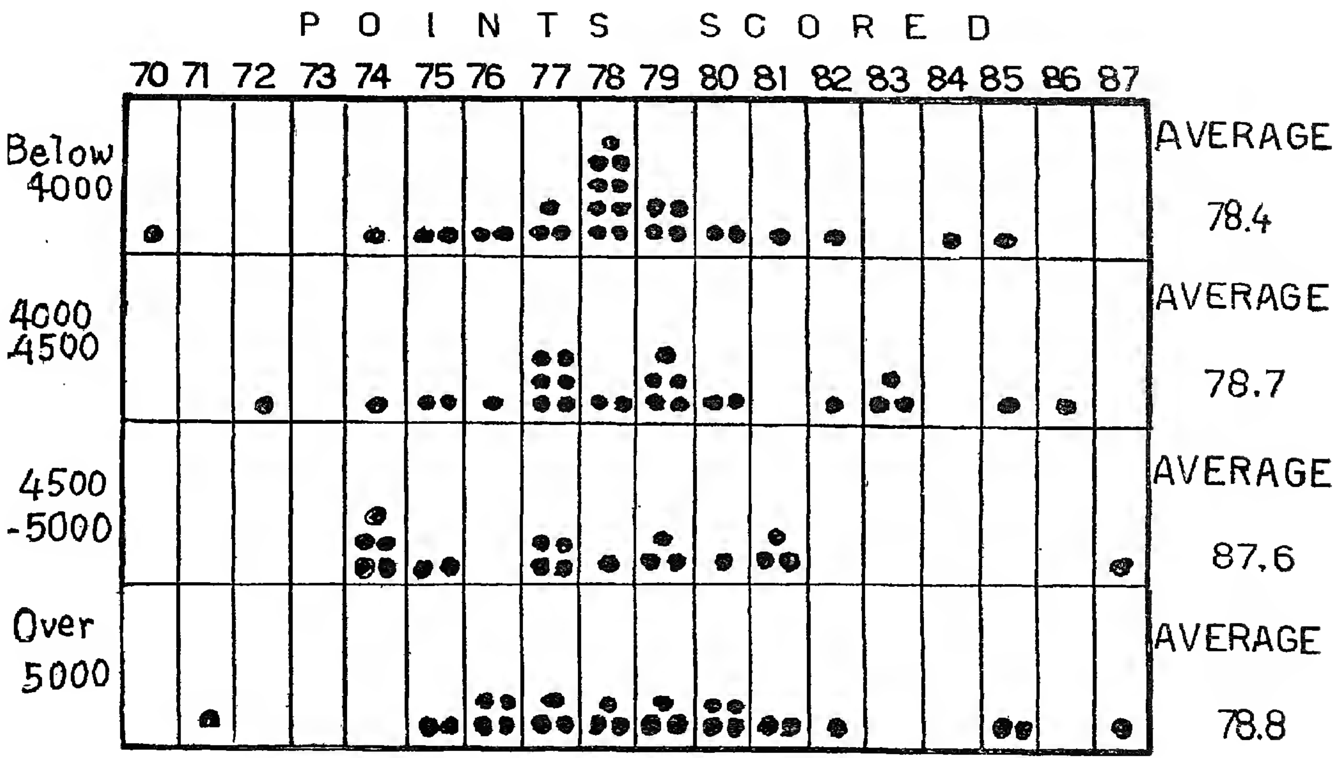

POINTS SCORED
70 71 72 73 74 75 76 77 78 79 80 81 82 83 84 85 86 87
Below 4000
4000 4500
4500 -5000
Over 5000
AVERAGE 78.4
AVERAGE 78.7
AVERAGE 87.6
AVERAGE 78.8

TABLE IB

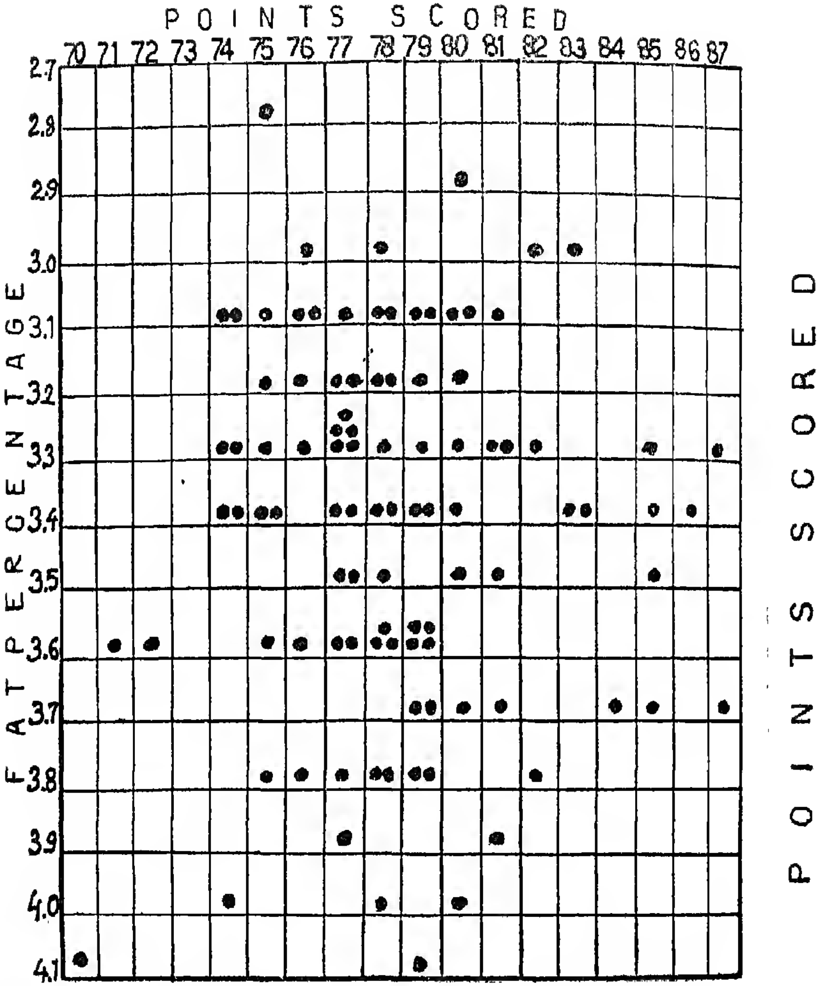

POINTS SCORED
70 71 72 73 74 75 76 77 78 79 80 81 82 83 84 85 86 87
FAT PERCENTAGE
2.7
2.8
2.9
3.0
3.1
3.2
3.3
3.4
3.5
3.6
3.7
3.8
3.9
4.0
4.1
POINTS SCORED

TABLE IIA

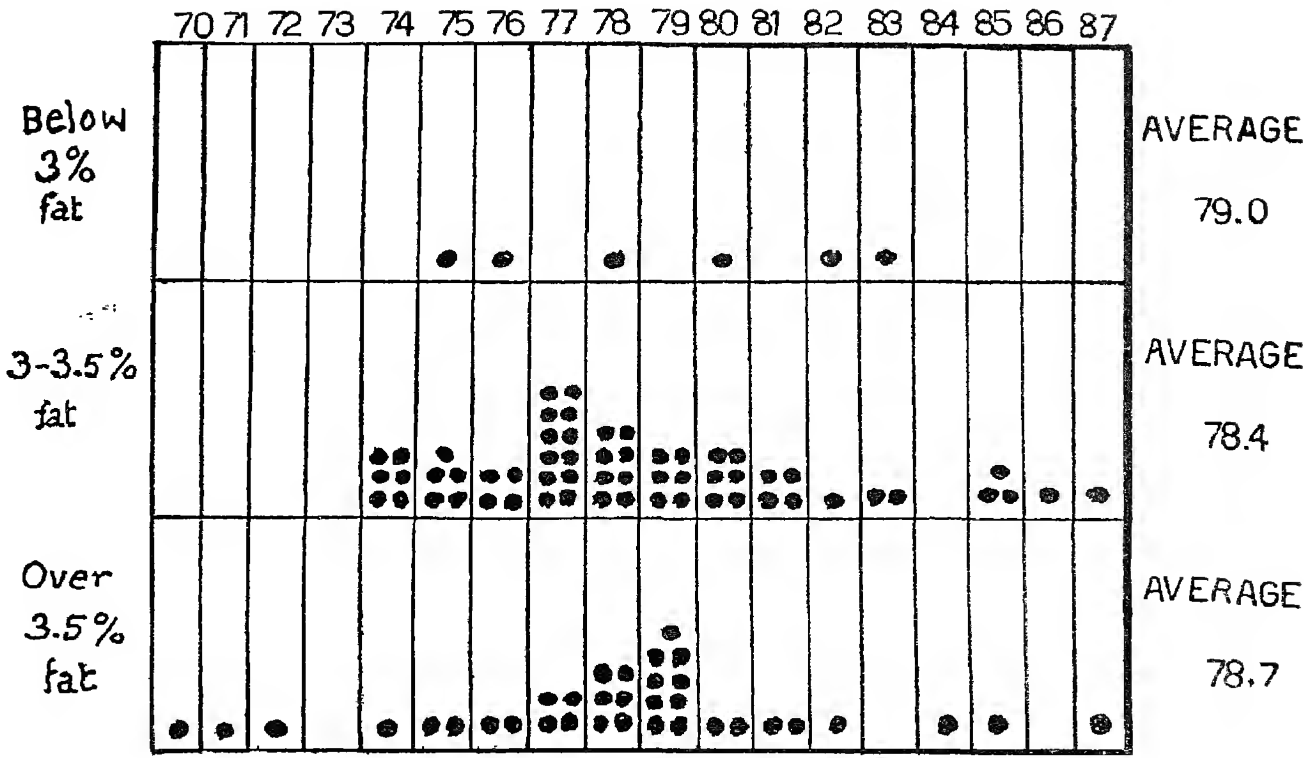

70 71 72 73 74 75 76 77 78 79 80 81 82 83 84 85 86 87
Below 3% fat
AVERAGE 79.0
3-3.5% fat
AVERAGE 78.4
Over 3.5% fat
AVERAGE 78.7

TABLE IIB

useful breed of domestic animals is an extremely dangerous and often very harmful thing. The conviction of the breeders of the old school that such standards are really an aid to selection because they are calling for characters correlated with economically-useful characters has no solid foundation.

Selection in such animals should be based almost entirely upon progeny-tests so designed as to point out the breeding animals that, by producing groups of valuable progeny, prove to have the correct inherited constitution. In polygamous animals the testing of females for economic value should give a basis on which to compare sires as breeders. In breeding such animals, a correct system of purifying the breed for that genotype which the useful animals should have makes the old system of selection according to fancied (or even real) correlative characters superfluous.

Selection according to such correlative characters is not only superfluous but extremely risky and often dangerous, for it slows up the process of purification of the breed.

In many of the continental herd-books for cattle, young stock can only be registered after they have passed an examination, in which points are given for different visible qualities. This makes it possible to judge whether any relation exists between those qualities the judges appreciate and real economic value.

A random group of consecutively numbered cows from the Friesland herd-book that had finished complete lactation periods has been grouped in tables according to the number of points scored and according to milk yield, especially fat percentage of their milk. The animals grouped in Table Ia have been divided in Table Ib into four groups at different levels of production. The cows in those groups average equal numbers of score-points.

In Table IIa the cows are arranged according to fat percentage and points. When we divide them into groups on different levels, as in Table IIb, the same average number of points is seen in each group.

We see from this that the choice between the selected, registered heifers and the rejected group does not help in any way to choose the better animals in the sense of those producing more or fatter milk. Subsequent findings do not justify this first choice. The scores of points of beauty and of utility have no relation to each other.

NOTES

"An arbitrary standard of show points in an economically useful breed of domestic animals is an extremely dangerous and often very harmful thing."

With this statement of Hagedoorn's no disinterested person who has studied the subject seriously would be inclined to disagree. There are too many known instances of the pursuit of breeders' fancy doing damage to the economic value of a breed.

Yet it must be admitted that show points arbitrarily chosen are something rather different from the appearance and performance of an individual animal, in other words, its phenotype, as an indication of its breeding value. While the value of such indications may be easily, and in some cases are rather foolishly, exaggerated, it would be wrong to assume that in every case they gave no indication of any value at all. Had they none then the sire performance tests of bulls and boars now being widely developed would be a patent waste of time, for what is being done there, without any question, is to utilize the phenotype of the sire as a reasonably reliable guide to his breeding value.

Where, however, the species is polygamous and yet only the female sex is usefully productive, as in the specialized breeds of egg-yielding poultry or dairy cattle, the phenotype of the male, obviously, can give little or no measure of his economic breeding value. The example, quoted by Hagedoorn, of the American Ayrshire breeders stopping the judging of bulls altogether, might be advantageously followed by many other breed societies. It is because of this difficulty presumably that Hagedoorn puts such very great stress upon both the value and the advisability of the progeny test. Thus, he wrote:

"Now, it ought to be clear to any disinterested observer, that from the moment we defer our judgment as to the breeding value of an animal to the time when we can actually measure this breeding value from the way the animal has performed as a breeder, all those methods that were destined to help us to guess the quality of a breeder, without watching the way it actually bred, have lost very much of their importance."

That argument would be perfectly sound were it not for the time involved, the expense incurred, and the difficulties liable to be encountered in making a reliable assessment of breeding merit by progeny testing. It is, in fact, largely as a time-saver and a money-saver that Sire Performance Tests are being employed as a substitute for, or a preliminary to, full-scale Progeny Tests in meat-yielding animals.

When Hagedoorn chose the title "Correlation" for this chapter I think he wished to emphasize the lack *of such correlation between an animal's individual appearance and breeding performance, between its phenotype and its breeding value dependent on its genotype. Perhaps he rather over-emphasized the point. If there were no such correlation, then ugly parents would have every bit as good a chance as have handsome parents of breeding good-looking children and yet, from common observation, we know that to be quite untrue.*

Chapter Twenty-Three

Constitution

A good animal, especially in those breeds that are kept for their performance or for their production, must have good constitution. If this word constitution means anything at all, it means very little else than inherited make-up, or genotype. It means that the animal, under favourable conditions, will be able to perform correctly, to produce economically, to do what we want it to do, and to keep on doing it without breaking down under the stress of what we expect of it.

The constitution of an animal can be judged by its performance, and not in any other way. This is very important, for necessarily there exist certain relations between the way an animal reacts to its life and the animal's appearance. An animal that is in heavy production and has the necessary constitution to enable it to stand up to this production is in very good health and shows this in its appearance, while another individual which cannot stand the strain does not look as healthy.

This does not necessarily mean that an animal that looks the picture of health has a good constitution. It is possible that the good-looking animal would not be able to stand the strain of an economically-profitable performance at all; it may be healthy-looking because its owner has been subjecting it to very little strain at all—it may have been fattened up for show purposes!

Only time will show whether a given animal has the correct constitution to stand the strain of use, but during the time it is in use something can be judged from its appearance. This fact has given rise to the idea that there is a direct connexion between an animal's looks and its constitution, but this idea is certainly erroneous. All we can tell by the looks of an animal

in full performance is whether it stands the strain well; but it is a mistake to think that by looking at an animal that is not or has not long been under the strain of performance, we can judge whether it has the correct constitution to stand this strain well in future.

Under the influence of the agricultural shows the appearance of our animals has assumed an importance out of all proportion to its real value. At the show nothing can be judged but the appearance of the moment, and for this reason the best animals at the show are simply those animals that for any reason please the judge best. The continual strain of heavy performance will gradually wear an animal down, and in the end it will alter the animal's appearance. It is evident that of two animals that have produced alike during the same period of time, we should have to judge that one the best which shows the least influence of this production. To be able to judge, however, we should first know that in reality those two animals had been producing alike for the same length of time under identical circumstances.

At the shows none of those conditions is fulfilled. The judge is set to compare a number of animals, of which he knows nothing at all, i.e. nothing except their appearance at the moment. To a certain extent his judgment depends upon fashion pure and simple, but insofar as he realizes that the breed judged is actually bred for economic usefulness, and insofar as he has seen animals of the breed keep up or break down under the stress of production, he will be likely to judge the class of animals as if the competing individuals had been subjected to the same strain. That is to say, he will be likely to favour the animals that look most like animals of excellent constitution under heavy production.

This, however, is not everything. Very often a spurious show-yard constitution will arise as an ideal in the mind of the show fanciers, which simply originated as the reverse of the signs of real constitutional defects.

A few instances of this can be gathered easily. A cow of poor constitution, that is producing more heavily than her body can stand, will be milked "off her legs", and one of the first signs of this may be a weak, tilted, splay foot. This is one of the reasons why judges of cows and bulls think a heavy cannon bone is beautiful as a sign of strength, of "constitution". A weak old cow that has been milked excessively may become rickety, her

legs will bend in and out, her back will sag. For this reason, strong, straight legs and a straight backline are taken as marks of excellent "constitution"; and because a poor, weak cow will get very thin when milking, fat, at the shows, is looked upon as a sign of "constitution"!

It is not very difficult to show that even if certain qualities may be actually signs of poor constitution in producing animals, the reverse, or what is taken as the reverse of those qualities, need not be taken as signs of excellent constitution. When we compare the foot of the Arabian horse with that of the Belgian, it is easily seen that mere circumference of the cannon bone is not correlated with strength of leg or foot. As Boutflour has repeatedly pointed out, the only two animals in which the back is really used to carry weight, and must therefore be strong, are the horse with a concave and the camel with a convex back, so we have no real reason to assume that straightness of back in a bull or cow denotes a strong back and good constitution. As soon as we look at other animals than cattle, when we compare different races of dogs, or even of man, we can obtain abundant proof that mere fat, or even mere muscle, does not prove a strong constitution. Nobody would dream of thinking that the greyhound has poor constitution as compared with the St. Bernard.

In poultry we have a very similar situation. Some hens, when they cannot stand the strain of heavy production, show the first signs of breaking down in their eye colour, which has a tendency to become pale. This, however, does not mean that in pullets that have not yet started to lay, good or bad constitution can be recognized by examining the eye colour. In poultry, good constitution, the ability to transform food into eggs economically and to continue doing this for many years is of great value, but the only way to recognize this good constitution is through observation of this continued production. Many people have sought short-cuts, and several systems have been proposed by which it was claimed one could recognize a good, profitable layer by means of characters of the individual. Sometimes qualities have been employed which directly result from egg production. In the yellow-shanked breeds, the yellow pigment gradually disappears in a hen in full production, and it reappears when laying is discontinued. To a certain extent it is possible to point out those hens in a flock which are in full lay,

and recognize them from the non-laying hens by looking at the intensity of the yellow colour of the shanks.

All those systems of recognizing good hens from poor ones by "handling" are less popular now than they used to be, for in the last few years it has been found that such poor-looking hens, which used to be culled out of the flocks, often did excellently when penned up separately in laying batteries. Many people have bought other people's "culls" cheaply and done very well with them in batteries, and it is very probable that the backwardness of such hens in large flocks is chiefly due to the fact that they are continually driven away from the food, and not to inability to stand the strain of heavy production when nourished well.

It is easy enough to see why the system of looking for signs of "constitution" when judging animals and birds at the shows has become established. Whereas it is very difficult to determine real "constitution" in the sense of ability to stand the strain of use, it is very easy to examine spurious marks of constitution at the inspection of a show animal.

In the showing of breeds of animals or birds that are of real economic importance, it is obvious that real economic value cannot be taken into account. A realization of this fact must ultimately produce a division between the "fancy", interested in show points as such, and the breeding of utility stock for economic purposes. There is more money in breeding for show purposes than there is in breeding utility stock, but the value of show stock is greatly enhanced if the breeders of fancy stock believe, and can make the utility breeders believe, that the fancy points judged at the shows are of great importance from the standpoint of the users of the stock.

There would be very much less interest in the judging of cattle, horses and swine at our agricultural shows if the public realized that show-yard excellence stands in no plausible relation to real economic value. The breeders of pedigree show stock want us to believe that what the judges are really looking for at the shows are signs of perfect constitution and "type", and that from an economic standpoint the prizewinning animals are far superior to the nondescript dairy cattle or work-horses at the farms.

It is rather difficult to look objectively at the present state of things. It is certain that breeding beautiful beasts pays better

than breeding good ones, and this greatly complicates the issue.

In only a very few instances can we compare the economic usefulness of beautiful animals with animals of lesser beauty. The best data can be found in those utility breeds of animals where there exists selective registration. In some herd-books young animals are not registered before they have been judged according to a scale of points. These scales are generally so arranged that the judge can allot a maximum of so many points to this quality, so many points to the relative beauty of that part of the body, and so on; and generally a minimum number of points is fixed below which an animal cannot be registered.

Where selective registration is the rule, we can compare large numbers of animals of two kinds, registered and unregistered. If it were true that the points valued by the judges were correlated with correct "constitution", so that the really good animals would generally pass the examination, whereas the inferior animals would be rejected, we would find that the group of registered animals would be significantly better from a purely utilitarian standpoint than the group of unregistered animals of similar parentage. This, however, is not the fact. Whenever we are able to compare two groups of cows milked at the same farms, one group comprising only registered and the other group consisting only of unregistered cows of similar parentage, we always find that the group of unregistered cows is just a little bit superior as compared with the group of more beautiful cows.

When we come to measure constitution we find exactly the same thing. If it were true that at the time of registration the judge really permitted the heifers of superior "constitution" to be registered, but rejected the others because their constitution was not as good, the registered groups would consist of stronger cows than the non-registered group.

It is not very easy to give a good measure of constitution in a dairy cow. One criterion we can apply is that of age: some cows are milked up to a certain age, other cows are milked longer. If we apply this test to the constitution of dairy cows in Holland, we find that in a study by Mr. Bosman on the quality of the mothers of stud bulls, the period during which cows were milked was calculated both for a group of registered and for a group of non-registered cows. The registered cows were milked

on the average somewhat shorter than the non-registered cows. His figures are very far from supporting the idea that at the moment of registration a distinction was made between the registered heifers of excellent constitution and the rejected group with inferior constitution.

I am very far from denying the importance of selective registration on show points as such; for a certain category of breeders this system is of great economic importance. If, however, we look at the system from the standpoint of the general user of the live stock, interested in cows and horses and sheep of excellent constitution, the system of selecting according to show points is of no value whatever. The contention of the supporters of the system that the judges are really selecting the young animals according to constitution is not supported by the facts.

In the long run the breeders will have to recognize that real economic quality in a domestic animal cannot be judged at a glance, and this will result in a split between breeding for show and breeding for utility. Wherever great masses of any domestic animal come into the hands of individual breeders, the tendency will be to select for real utility and neglect real show points. A good instance is that of utility poultry and utility ducks. In poultry breeding the breeding of show birds has been almost wholly divorced from the breeding of utility poultry. This is often true of the same breed. The breeders of show White Leghorns are greatly concerned about the shape and colour of the ears, about the points of the comb, carriage of the tail, colour of the eyes, etc. They are not interested in early maturity or in number or size of the eggs.

The breeders of utility Leghorns should be indifferent toward all those points, and concern themselves only with qualities that give the breed its economic value. In reality, in many instances the breeders of utility poultry give too much attention to irrelevant fancy points that are believed to be marks of "constitution". Eye colour has often been the fashion.

NOTES

Although an excellently argued chapter, I am not altogether happy that its title is entirely appropriate. It seems to me that what Hagedoorn is mainly concerned with here is the point to which he repeatedly returns, namely, the

gulf that too frequently separates show-yard standards from economic utility. With that contention I am in entire agreement. I also agree with Hagedoorn's verdict that show-yard judges are inclined to speak of "constitution" when in fact they are dealing with points of breeder's fancy. Yet, is it true to say that the somewhat vaguely defined term "constitution" as applied to livestock is entirely a matter of breeders' fancy? I am not at all convinced that it is.

My main reason for saying so is that I have heard the word "constitution" used by livestock breeders who never entered a single animal for show. I have heard the term "lack of constitution" used as a criticism of pedigreed stock in general and of prize-winning livestock in particular. Whether the conception of "constitution" in livestock is nonsensical or otherwise it cannot, therefore, be entirely an attempted economic justification of breeder's conventional standards of show-yard excellence.

It seems to me that the term "constitution" in livestock is one mainly descriptive of health and vitality. It is one difficult to define, yet Hagedoorn himself provides a quite reasonable definition:

"It means that the animal, under favourable conditions, will be able to perform correctly, to produce economically, to do what we want it to do, and to keep on doing it without breaking down under the stress of what we expect of it." He then goes on to say, "The constitution of an animal can be judged by its performance, and not in any other way."

Again, this is at least partly true. Performance is the ultimate test of a sound constitution, but what possible guidance can it give to a man buying stock, particularly young livestock which have never had the opportunity to perform? Are there no other signs of a sound constitution or the reverse? I think that there are, and that is why I cannot agree with Hagedoorn's statement that it is ". . . a mistake to think that by looking at an animal that is not or has not long been under the strain of performance we can judge whether it has the correct constitution to stand this strain well in future."

Surely this statement is somewhat of an exaggeration! Were it strictly true a knock-kneed heifer or a wether-headed ewe lamb would be a safe breeding proposition to buy. Yet neither is anything of the kind. There may be, and in my view there are, many other signs, some rather subtle, which give useful guidance to an animal's future performance. I speak purely from personal experience but I have never, for example, known a pink-nosed Border Leicester sheep that wasn't delicate, and in store cattle I have a distrust of those that are entirely white. In Scottish Blackface rams there is occasionally a balance, an energy, a vibrating vitality, which attracts the eye of the experienced buyer as well as that of the show-yard judge. There are ewes in some breeds that by their facial expression give promise of abundant lambs and milk. Others do not. Is that sort of statement personal prejudice or experience of husbandry? I should not care to be dogmatic on the subject, but of one thing I am sure. Constitution is something different from show-yard appearance.

Chapter Twenty-Four

Herd-books

The purpose of a herd-book should be to make it possible for a large group of breeders to co-operate in the breeding of some class of animal when conditions are such that they cannot very well undertake this task by themselves.

For breeders of agricultural plants, where each breeder can ameliorate his own breeding stock without recourse to the material owned by anybody else, or even for breeders of ducks or poultry, which are bred in hundreds or thousands of individuals, herd-books would be of very little value. Most breeders of cattle or of horses, however, can keep only a very restricted number of animals economically, and in order to partake in the work of perfecting the breed he is interested in, a breeder must be able to get data on the breeding and personal merits of the other man's breeding stock which are as complete as the data of his own animals.

Herd-books, stud-books, flock-books vary very much in method of procedure and in completeness of the data registered. The ideal herd-book would be the one that would give complete data about all the animals of the breed, their ancestors and descendants. As far as possible a herd-book should not restrict its activity to registering the excellent animals of the breed, but it should record every animal, and when economically useful animals are concerned its record of performance as well.

The real purpose of a herd-book is to furnish us with data which give an insight into the inherited make-up of the available breeding animals. Records concerning ancestors are of value in giving us an idea about the performance and especially about the breeding value we can expect of an individual. Records about the descendants of breeding animals are clearly

of far greater value than records about the ancestors. This is especially true when we are dealing with animals that are still living and available for breeding purposes.

Most herd-books only register animals of a given level of merit, and this restricts their value considerably. The purpose of this method is twofold: in the first place it restricts the work to be performed by the officers of the herd-book society, and in the second place it helps the selection of valuable animals in the interest of ameliorating the breed.

Before we knew much about the mechanism of heredity it was commonly believed that the qualities of an ancestor directly influenced the quality of his descendants, so that it was important for the owner of an animal to be able to show an official pedigree in which a long list of direct ancestors were listed, each one more perfect than the preceding one.

Selective registration, the recording of excellent individuals and the rejection of poor ones, has the advantages named, but its disadvantages more than counterbalance its doubtful merits.

A breeding animal, especially a male that has been used extensively, produces a variable lot of descendants, some excellent, some good, some fair, some of poor value. If we can find just what kind of daughters a bull has produced from a given number of cows whose quality is also recorded, we get a very good insight into his value as a breeder. When, however, the daughters registered are a selected group of exclusively good ones, the data are incomplete and as a result may be practically worthless. When we see from the books that a bull has ten excellent daughters, it might make a great deal of difference to our deductions if we knew whether these ten are a selected group out of twelve daughters produced by that father, or whether the ten are the only good ones in a hundred!

If a breeder of laying hens were to record only his excellent producers, and scrap not only his poor hens, but also their records of performance, he would greatly hamper his own progress, as he would never be able to judge his breeding males correctly as such.

Continental herd-books of farm animals generally use a system of selective registration, whereas the English and American herd-book leaves it to the breeders which animals they want to register. Both systems have their faults. The system of registering only the animals selected by the herd-book officials

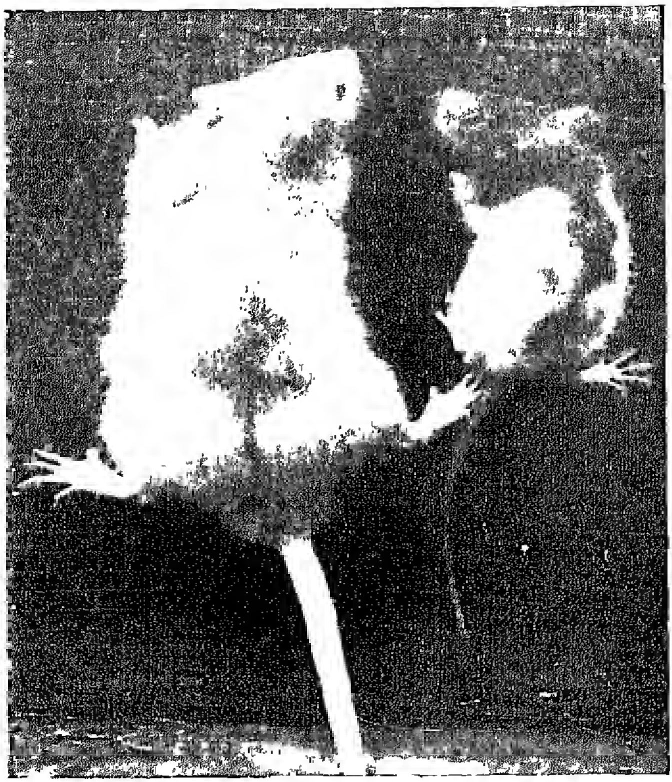


FIG. 2.—Two full brothers, litter mates, at eight weeks. The dwarf weighs 40 per cent. of his normal brother's weight. These dwarfs occur in a proportion of one in sixteen in the second generation of a cross between two normal strains. Dwarfism seems to be an instance of a double recessive novum. Such instances are often mistaken for cases of mutation. In rats the dwarfs are fully viable. (See p. 34.)

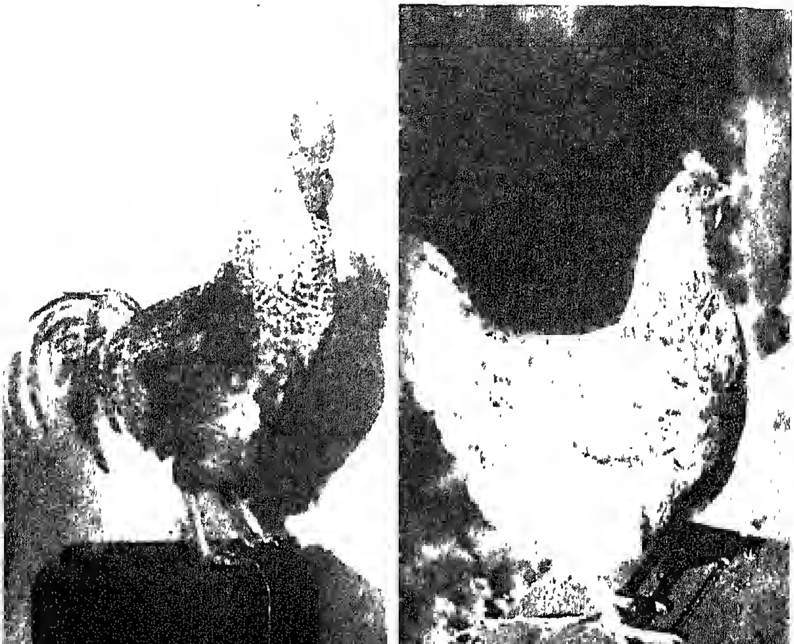


Fig. 6.—The Autosexing Barnevelder, produced by adding the "barring" gene to a good strain of Barnevelders, by a system of repeated back-crosses. The males, being homozygous for the gene, are born whitish and grow up light barred; the females, being haplozygous, are born brown striped and grow up greyish brown. The sexes can be readily distinguished at birth. (See p. 52.)

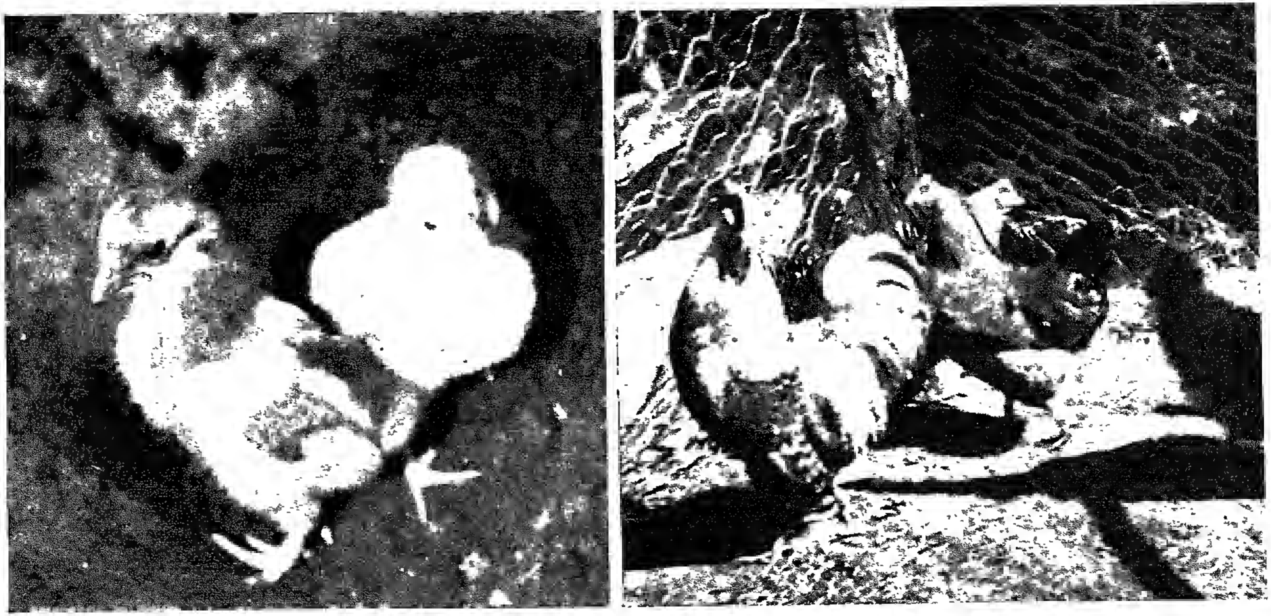
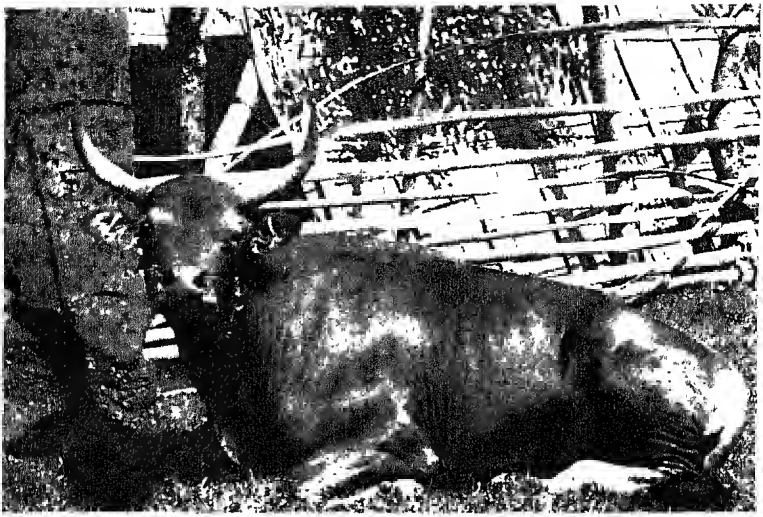


Fig. 8.—Autosexing Barnevelders. *Left:* male (greyish buff) and female (brown) chicks. *Right:* adults.

The colour of the chicks, which was rather variable during the first few generations, has become constant when after many back-crosses to pure Barnevelders the breed assumed the residual genotype of the Barnevelder, with only the sex chromosome containing the barring factor substituted for the common one in Barnevelders, which lacks this gene. It is possible that the complete absence of broodiness is due to one or more other sex-linked genes carried in this sex chromosome, which was taken from the Tancred strain of White Leghorn. (See p. 53.)

FIG. 9.—Litter of mice containing dwarfs. Of the thirteen young mice one dwarf has died, the remaining two are the second from the left and the animal lying across the others. Age nine days. In this family the dwarfs differ from normals in one gene. Very few dwarfs are raised to maturity. (See p. 118.)



(*Photo by courtesy of J. Jeswiet.*)

FIG. 10.—First generation cross bull, father Madurese, mother Javanese. Many of these very active hybrid bulls are bred in the east part of Java for carting and for the popular sport of bull-racing. (See p. 93.)

FIG. 11.—Barré v. d. Kilstroom, one of Mr. Saarloos' Alsatian × Wolf hybrids at the age of six months. The modern police dog owes many of its good qualities to the introduction of wolf genes into the German shepherd breed. These hybrids are fertile in both sexes. (See p. 316.)

(*Photo by courtesy of Mr. J. Kaan, Wieringerwaard, Holland.*)

FIG. 14.—When cross-bred ewes produced by grading the local, short-tailed breed of the island of Wieringen to Texels, were bred to a full brother, a number of deformed lambs were born with the lower part of all four legs missing (p. 120).

(*Photo: R. van Vloten.*)

FIG. 15.—Scrotal hernia in piglets. Some boars, when mated to certain sows, produce approximately 25 per cent. of herniated male offspring. Such boars, 50 per cent. of whose sperm is affected, should not be used for further breeding, and their otherwise superior sons should be tested. This can easily be done by mating them to sows that have shown (by the production of abnormal piglets) that they are heterozygous. Test-mating old boars to their own daughters will show up their impurity in this respect as well as their purity or otherwise in regard to all other genes for which we want our breeding stock to be pure. (See p. 121.)

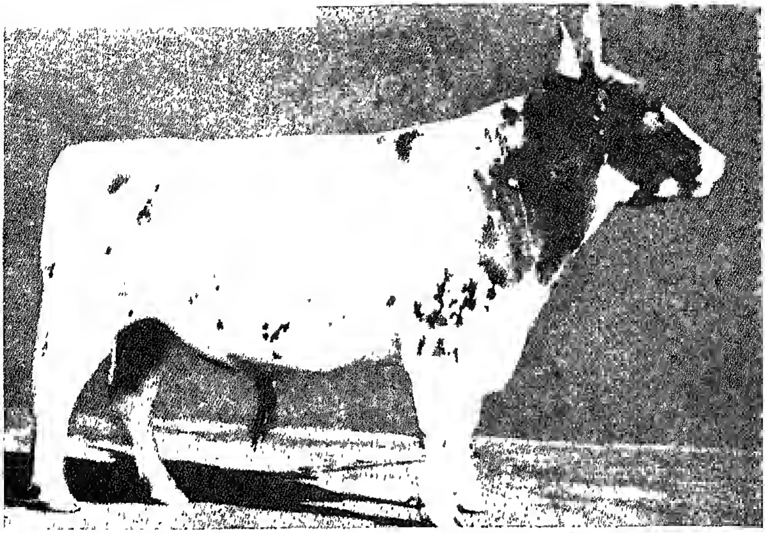
FIG. 16.—Red Danish bull, HOTHER 9,539, at the breeding farm of Kolle Kolle, Denmark. Hother's ten oldest daughters averaged 4.730 kg. milk with 4·31 per cent. fat. Aged ten years when photographed by the author. (See p. 123).

(*Picture and records by courtesy of Mr. J. Hunter-Smith, Herts Institute of Agriculture.*)

FIG. 17.—Ayrshire Bull AUCHENDRANE SIR MINSTREL. His daughters in the Auchendrane herd produced as heifers in the first lactation period: 20 daughters, aver. 1,016 gal., 3·96 per cent. fat. (Dams, first lact. 985 gal. and 4·12 per cent. fat.)

In the Kirkhill herd, 18 daughters produced 967 gallons, 3·83 per cent. (dams 716 gal., 4·04 per cent. fat). Total 38 daughters, aver. 993 gal., 3·89 per cent. fat.

Between the average records of his two sets of daughters there is only a difference of 59 gal. and 0·13 per cent. fat. When we calculate his Mount Hope (intermediate) index by comparing daughters to dams, we get 1,198 gal., 3·62 per cent. fat in the Kirkdale, and 1,047 gal., 3·80 per cent. fat in the Auchendrane stock, which gives a difference of 151 gallons and 0·16 per cent. fat. In this bull the average of the daughters' records alone gives us a better picture of his genotype (breeding value) than a complicated index that takes account of the dam's records. (See p. 123.)



(*Picture and records by courtesy of Mr. J. Hunter-Smith.*)

FIG. 18.—Ayrshire Bull CARNELL FOOTPRINT, property of the Hannah Dairy Research Institute, Scotland.

Thirty-two daughters from this bull averaged 1,037 gallons, 4·10 per cent. fat during their first lactation (dams 726 gal., 3·87 per cent. fat).

A daughter-dam comparison would give him an index of 1,348 gal., 4·33 per cent. fat, but this would not give as good an indication of his genotype as the plain daughter-average. (See p. 187.)

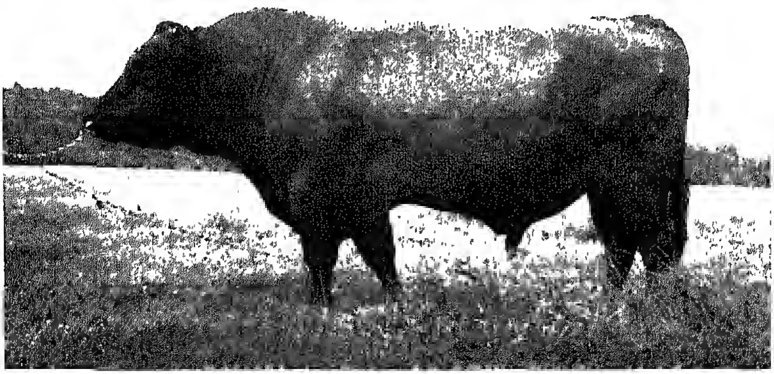
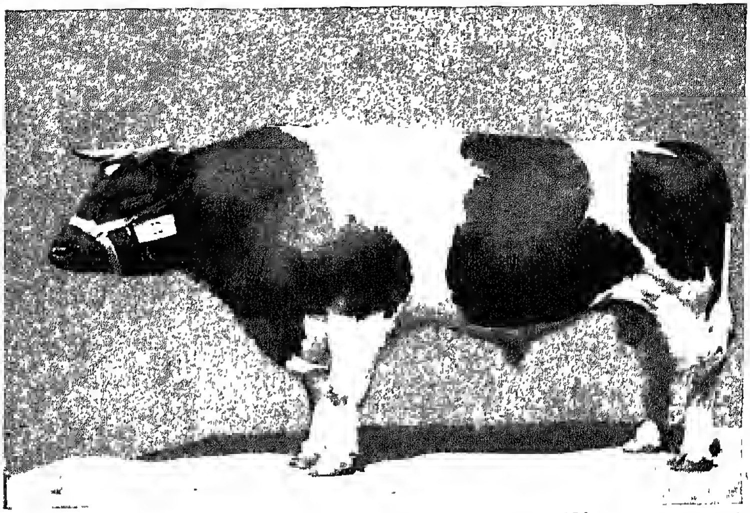


FIG. 19.—By courtesy of Prof. Øjvind Winge, Kopenhagen, is shown Kolle Kolle's best bull, HØJVIG 136, Herdbook 3622. This bull has been used at Kolle Kolle in Denmark from 1940 till 1952, Twenty-one daughters of this bull, during 31 lactations, averaged 5,121 kg. milk, 4·33 per cent. fat, or 249 kg. butter. Born September 3, 1938, died October, 1952. (See p. 187.)



(*Photo: A. Bruyning.*)

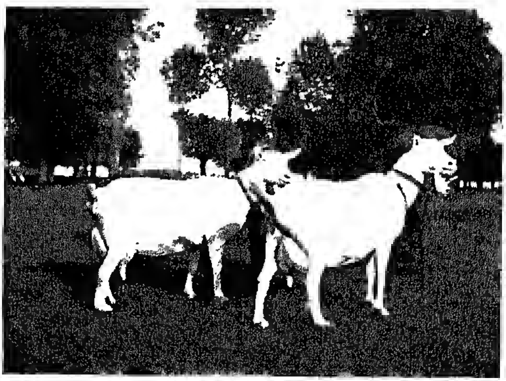
FIG. 20.—ADEMA'S ATHLEET, born February 24, 1929, breeder S. A. Knol, Hartwerd, Holland.

This bull scored 83 points in the Friesian herd-book (F.R.S. 18,300) and 85·5 points in the Netherland herd-book (N.R.S. 13,817).

He was declared "preferent" after an examination of his progeny, in 1934.

When he was five years old, he had eight daughters, averaging 6,962 lb. milk with 3·87 per cent. fat, *first lactation*. He was then bought by the Co-operative Breeding Society in Lonneker-Enschede.

The average production of his first 100 daughters (first lactation) was 7,586 lb. of milk with 4·05 per cent. fat in 330 days. (See p. 187.)



(*Photograph by the Society's Secretary, Mr. J. Versluis, Serooskerke, 1926.*)

FIG. 21.—The Society for improving the goats in the province of Zeeland, Holland, evaluates the animals according to their ability to give milk cheaply over an extended lactation period. Males are evaluated according to the quality of their progeny. Goats owned by J. Verpoorte, Axel. (See p. 326.)

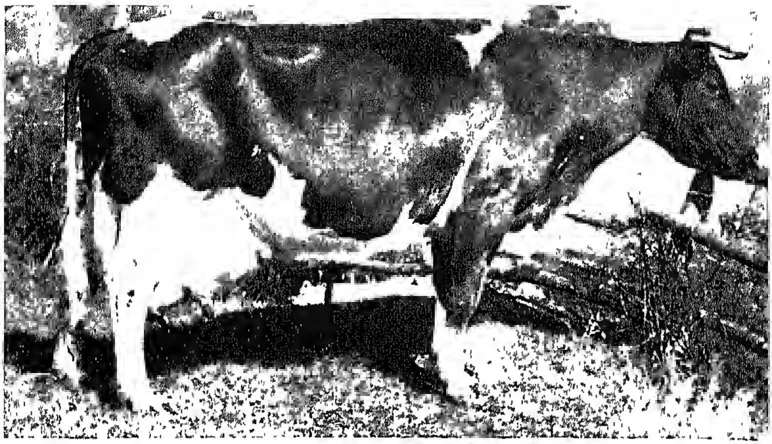


FIG. 23.—Manningford Faith Jan Graceful.

Manningford Faith Jan Graceful, British Friesian, is the world leader for aggregate milk production; by December 6, 1953, at 15 years 7 months old, she had totalled 313,928 lb. milk. This includes milk in excess of 365 day lactations; eight of her lactations have exceeded 20,000 lb., of which five exceeded 30,000 lb.

She is the result of a half-brother–sister mating. Bred by Geo. M. Odlum and owned and developed by R. and H. Jenkinson.

Her sire, Manningford Faith Jan R.M. (died early in 1950), with his first 51 daughters milked, had a first lactation average for 365 days, on 2X of 12,918 lb. of milk at 3·65 per cent. Perhaps another 20 daughters have since been milked: of these daughters, to date 28 have had lactations exceeding 20,000 lb. with at least 62 such lactations. By May 1953, 61 daughters were R.M. with 134 entries averaging around 15,600 lb. milk with 3·78 per cent. fat. (See p. 223.)

FIG. 24.—Prof. O. L. Mohr of the University of Oslo, Norway, has kindly lent the picture of an "amputated" calf with a very distorted skull and hardly any legs, and of a calf with an extremely shortened neck.

In both cases the aberration was lethal and recessive. (See p. 121.)

Fig. 25.—Staby male "Durk". Photograph sent by Mr. Aukema. The villages in the province of Friesland have had their local dogs for many dog generations. These are mostly black and white or chocolate and white.

The "Staby" is kept as an all-round intelligent farm dog and watch dog, and is used as a Spaniel for shooting over, staying close to the man.

It will keep an eye on the stock and the children and help the farmer or his men to keep down moles. It has become a popular dog in the cities, and at the dog shows. It is now decidedly more variable than the "Wetterhoun". (See p. 104.)

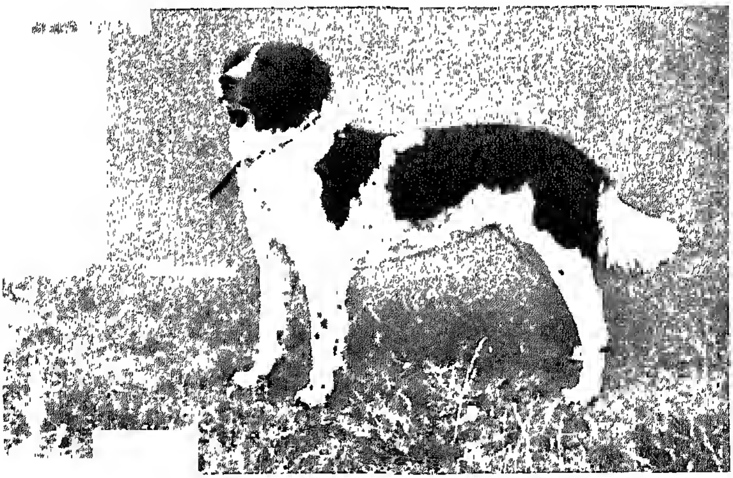


Fig. 26.—Wetterhoun male "Joep", owned by Mr. Fraenkel. Photo sent by Mr. Aukema. The "Wetterhoun" (Friesian waterdog) is larger than the Staby. The fanciers of this breed, farmers and farm labourers, take their dogs out in the dark of the night for hunting the numerous polecats (and sometimes poaching the rare otters) of the marshy districts around the Friesland lakes. The dogs do this work single-handed, killing and bringing their catch to their masters. The owners care nothing for the appearance of their animals, but will go long distances to patronize sires famous for their staying powers and courage. The breed is decidedly more uniform and true to type than the Staby, perhaps as a consequence of this.

Coat curly, colours black or chocolate. (See p. 104.)

(*Copyright Particam Pictures.*)

FIG. 27.—Coming from the station for a busy day's work in Amsterdam. A lady with her dog taking her through heavy traffic at a busy hour.
See the section on "Dogs to lead the Blind" (p. 315).

FIG. 28.—Wirehaired fox terrier with standing ears. (See p. 313.)

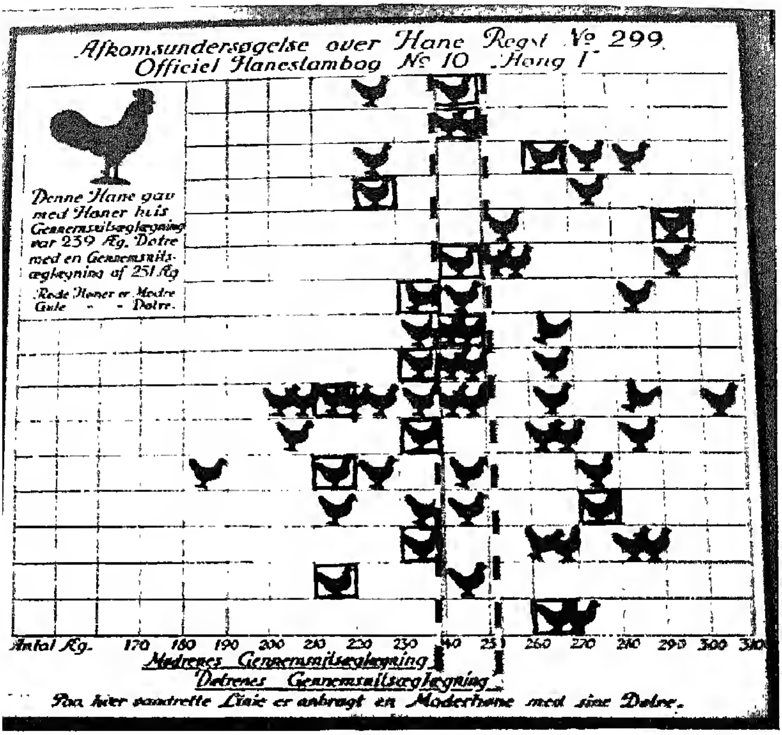


FIG. 29.

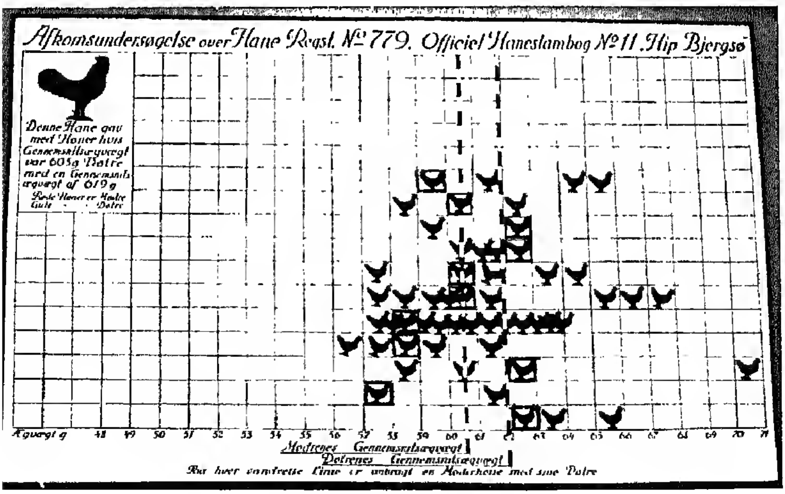
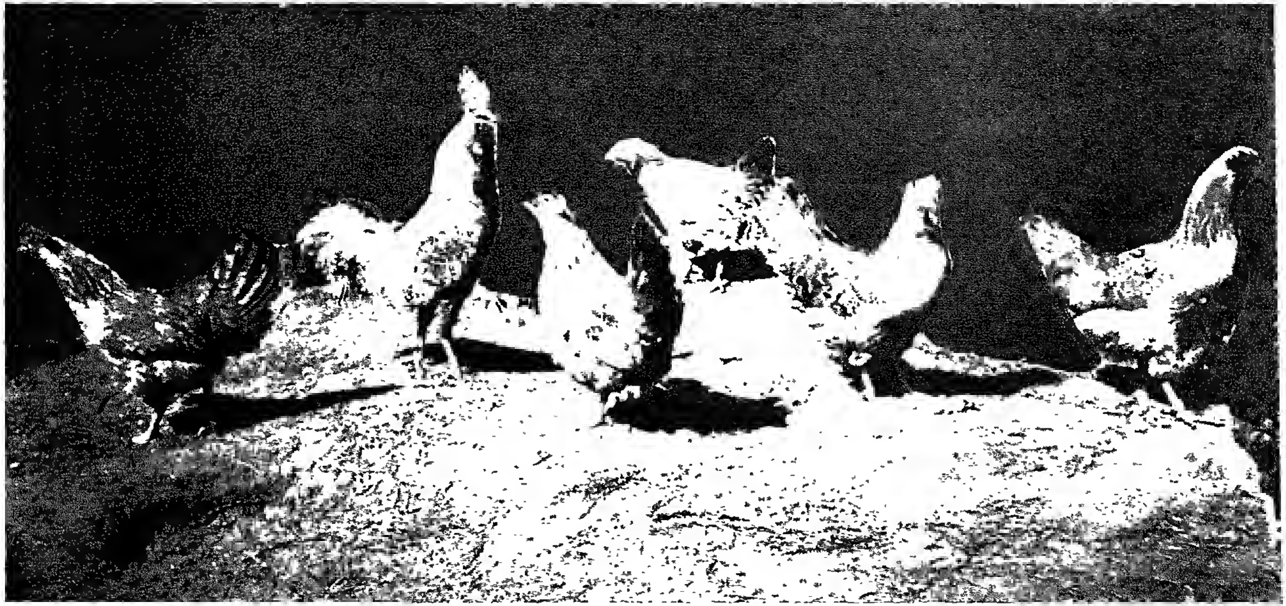


FIG. 30. (See p. 321.)

(For descriptions of these graphs see foot of page 189)



(*Photograph by the author, 1936.*)

FIG. 31.—The *Autosexing Leghorn*, produced by combining the colouring of the so-called wild-coloured Leghorn (a show breed that contains the "barring" factor) with the egg production of an excellent strain of Brown Leghorn.

Prof. Punnett has produced a group of cross-bred poultry from Leghorn crossed to Plymouth Rock, which is very similar in colour, and which he has named the "Legbar".

Colour of the chicks in the pure strain: whitish for males, brown striped in females; eggs large, chalk-white, complete absence of broodiness. (See p. 52.)

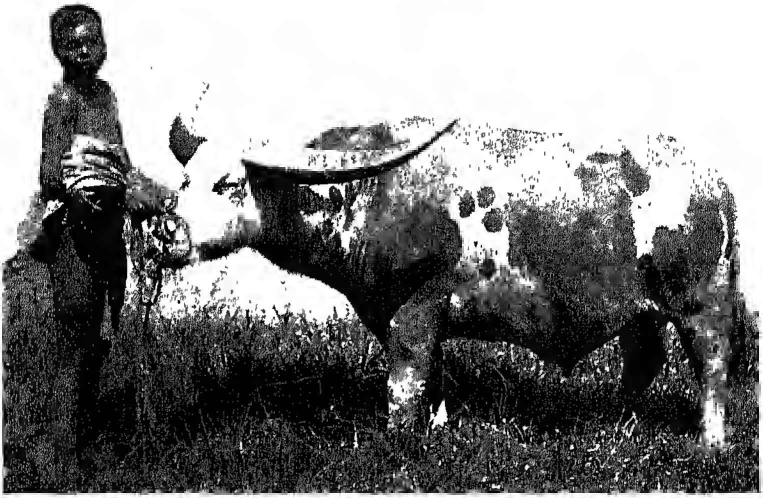
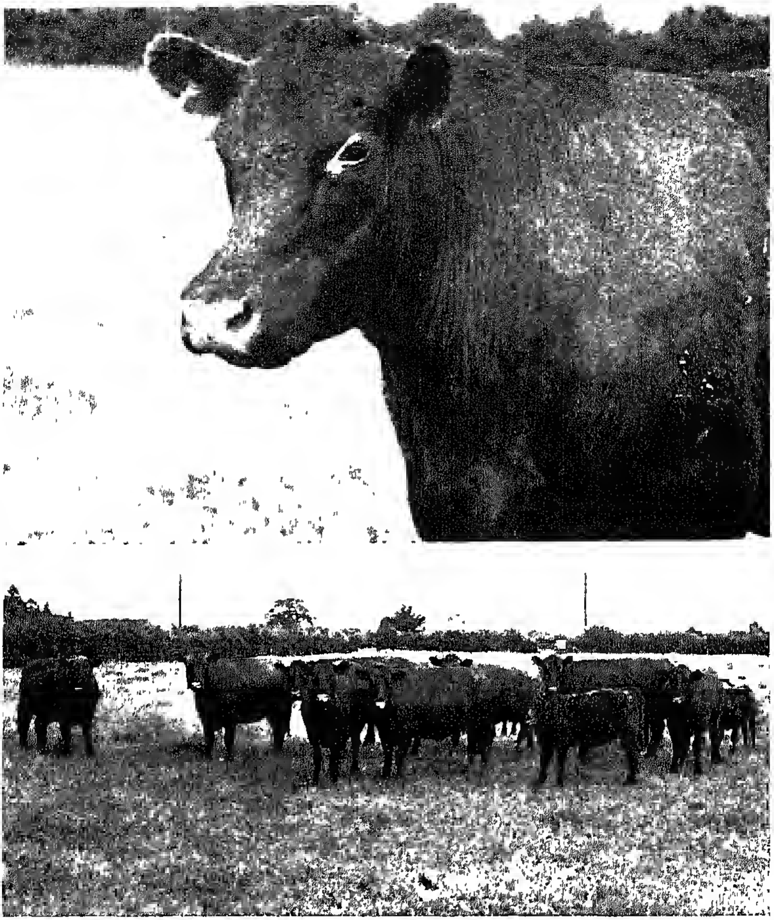


FIG. 32.—Spotted water-buffalo belonging to the head of Rante Pao. Animals of this strain are used by the Sadang Toradjas in the procession at the festival of the dead. (See p. 324.)



(*Photo: "Farmer & Stockbreeder".*)

FIG. 33.—Mr. Eric L. C. Pentecost's Polled Lincoln Red Shorthorns.
Above: Heifer No. S 17.

Mr. Pentecost is deliberately dehorning a well-known breed by the adding of a gene from another breed (or substituting a chromosome that carries it).

After some correspondence he used Red Aberdeen Angus males for the purpose and then back-crossed the polled females for four and five generations to males of Lincoln Red Shorthorn, continuing from the polled ones.

His work has now progressed so far that the Lincoln Red Shorthorn Society has made an agreement with him, so that the herd-book will get the benefit of his work. Some polled heifers will be entered as foundation females of a new polled breed (or section).

With regard to bulls, only bulls homozygous for polling may be registered with the Society, for it is Mr. Pentecost's object, with which the Herd-book council agrees, to make this separate polled section breed true as to polling like Aberdeen Angus or Galloway. For this reason only proven homozygotes will be accepted from the beginning. (See p. 230.)

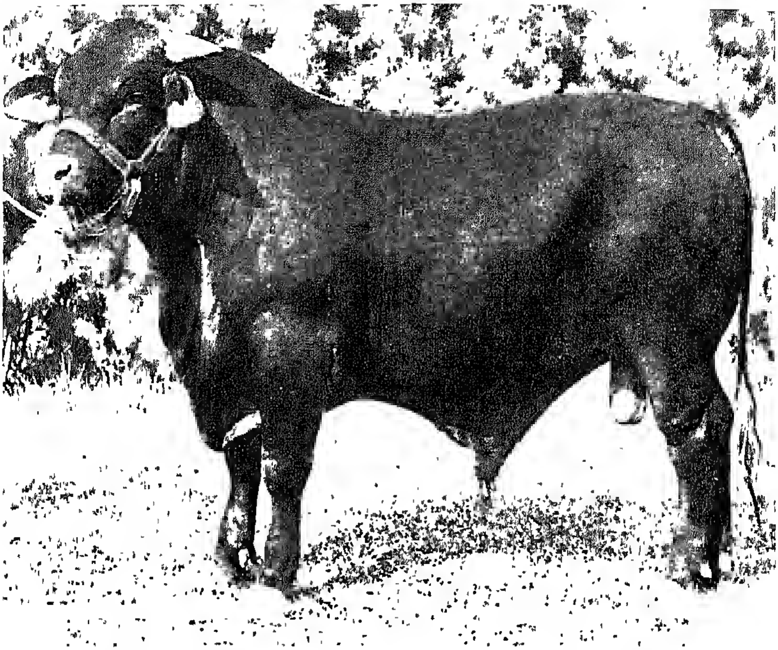


FIG. 34.—Santa Gertrudis bull—approximately 18 months of age.

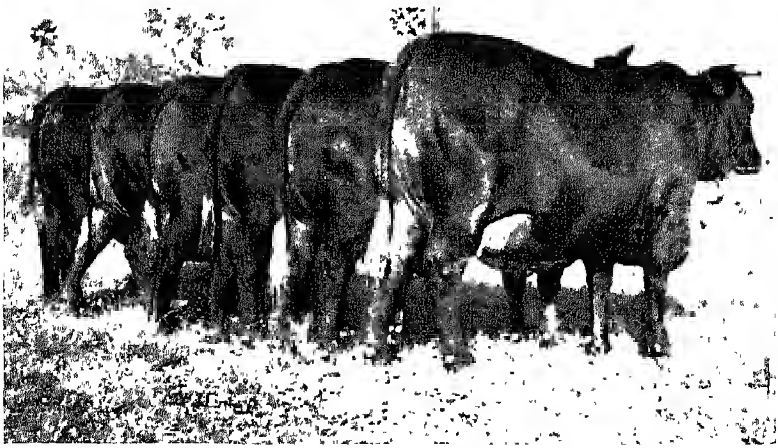


FIG. 35.—Santa Gertrudis show heifers, age 2 years old. Weight: 1,305 lb., 1,620 lb., 1,275 lb., 1,400 lb., 1,450 lb., 1,400 lb. (See p. 306.)

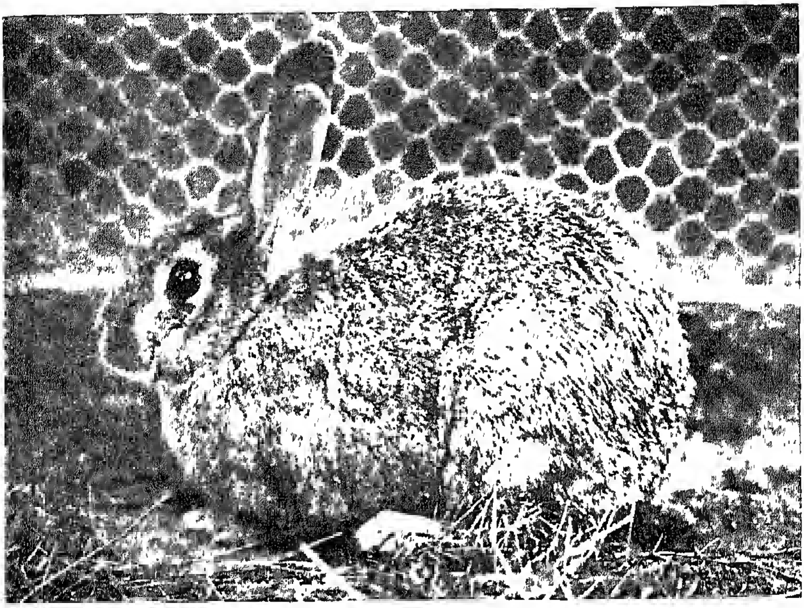
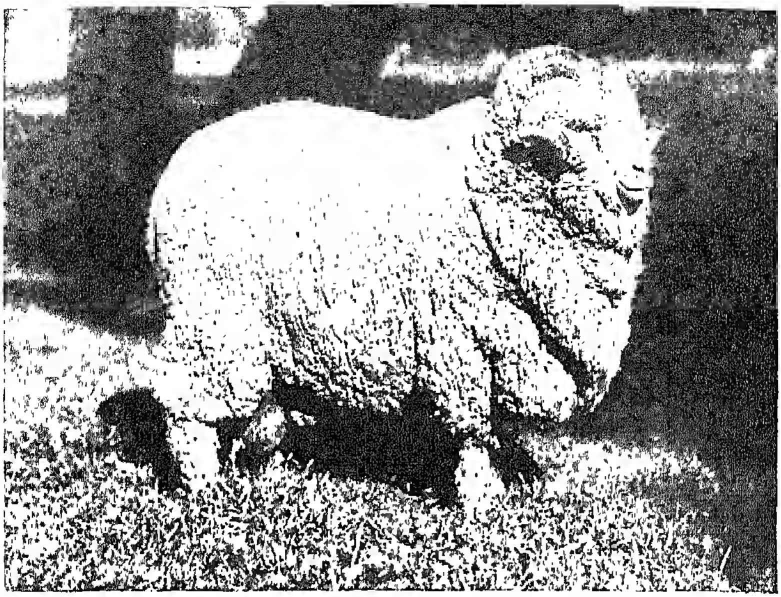


Fig. 36.—Female hybrid (leporid) bred by Mr. van Dyk in Doorn, Holland, from a pet doe hare and a buck rabbit. (See p. 296.)

This doe was born with two other hybrids after the hare had been pregnant for over five weeks, the young being born with the eyes open, like leverets. The hybrid doe photographed was quite tameable, and fully fertile.

Mated to a Belgian hare buck, some of the young were russet, some rabbit grey like this doe. A striking point about leporids is that evidently the genotype of the mother determines the length of the pregnancy, and that they are equally viable when born after four weeks, naked, in a doe rabbit's nest as two or three weeks later, much further developed, when the doe hare is the mother of the hybrids. All hybrids with one hare parent handled were tameable, like the hare, while hybrids with one wild rabbit parent were hopelessly untameable. (See p. 319.)



(*The Land*, N.S. Wales.)

Boonoke (New South Wales) Horned Ram.

(*The Land*, N.S. Wales.)

FIG. 37.—Boonoke Polled Rams. Bred by T. S. Falkiner & Sons (See p. 230)

is faulty in that it restricts the registration to fewer animals than are utilized in the breed, and so restricts the data about the parents, which in itself is to be regretted.

The idea of registering only the good animals is laudable in principle, but in actual practice it really means that a certain number of animals are rejected because they do not happen to come up to certain preconceived notions of how a young horse or bull should look. The selection at the time of registration is chiefly upon points of beauty, which have no obvious connexion with utility and which have repeatedly been shown not to be so connected.

In the herd-books, which register only the most beautiful young animals, very often a separate register is kept in which births are registered, so-called calf-books. In certain instances, as in the N.R.S. and F.R.S. in Holland, heifers registered in *this calf-book, even if they have not been eligible for the herd-*book, are considered as pure-bred, and their offspring from registered bulls are eligible for registration in the herd-book. This is a step in the right direction, but obviously it is better to register everything and to leave the selection to the breeders themselves.

Voluntary registration, as in English and American herd-books, has the advantage that no animals from pure-bred parents are rejected, so that the data about the breeding of the parents could be more complete. This system is not ideal, because many young animals are never registered because the owners do not consider them worth the trouble. Evidently the ideal system of registration would be one in which every animal born was registered, so that every breeder could obtain full records of the breeding results from all the animals used for breeding in the herds.

The importance of full records about the ancestry of breeding animals has been grossly overrated. It is very much more important to know what sort of descendants an animal has, than to know what the quality of his ancestors has been. The only value of importance the pedigree of an animal generally has is to furnish proof that the animal is not cross-bred. Examining a pedigree we look backwards, and it is much more important to look forward into the future.

Some herd-books are closed, that is to say that it is impossible to register an animal whose parents are not both registered

pure-breds. There exist, however, a good many herd-books that are open to the extent that in certain conditions they will accept animals the ancestry of which is not proved.

There are various ways of doing things. In the *Dutch Dog Stud-book* (*N.H.S.B.*) an animal could formerly be entered after it had earned a certain qualification in the shows a certain number of times. Some herd-books have special registers for animals without proved ancestors, and the offspring of those animals can be registered in the ordinary herd-books. In the *N.R.S. Dutch Cattle Herd-book*, specially beautiful heifers may be registered in a special register, and their calves from registered bulls may be entered in the ordinary register. Some horse stud-books are not hermetically closed against the acceptance of animals, the pedigree of which is not proved.

The advantage of an open stud-book is obvious when the proportion of registered to unregistered animals in a breed is unfavourable. When the herd-book is started and the majority of animals are still outside, it will be of great advantage to accept the very best animals into the stud as soon as possible. Another advantage of making the entrance of unproved animals possible may lie in the possibility of admitting animals of outstanding merit that can be useful in helping to improve the breed still further.

When, however, no excellent animals belonging to the breed exist outside the herd-book, there is no real reason for not closing the book to outside animals. In practice this seems to be the most general argument for keeping the stud-book open or for closing it.

When a breed of animals is imported from some foreign country, there is every reason for closing the registration to any animals outside the imported group or their descendants. In accordance with this, to give a few examples, the American herd-book of the Holstein-Friesian Association was closed from the beginning, with the exception of a few cattle imported from Holland. The Dutch herd-books remained open, and are still open.

There seems no good reason for keeping those herd-books open other than the fact that, as the registration is selective, a good many pure-bred bulls and heifers are dropped from the books continually. This produces a mass of unregistered animals which are really pure-bred, and keeping the herd-book open

allows of re-entering this material at a later generation. If, however, the inspection for show points at registration, which now keeps out about 10 per cent. of the heifers and 40 per cent. of the bulls, were discontinued, there would be no object in keeping the herd-book open for registration of any but the offspring of registered parents.

In the last few years the question of registration of high grades in cattle herd-books has been much discussed. In Holland, where good-looking grades can be registered, some people (among whom I range myself) want the herd-books to be closed; in England some breeders like to permit the registration of excellent high grades.

An ideal solution of the difficulty is to make a ruling by which it is possible to register grades in a special register. If we do this it becomes possible to prove the pedigree of the higher-grade animals. We can then accept as pure-bred those animals whose non-registered ancestor dates back for a certain number of generations, five or six. In this way it becomes possible to make use of the superior quality of an exceptionally good grade, without heightening the variability of the pure-bred stock.

The *Dutch Dog Stud-book* has made this change in its regulations with very satisfactory results. It is very important that only animals with a proven ancestry of at least five back-crosses to pure-bred sires shall be admitted—a superficial examination of the looks of a grade animal should never be used as a basis for acceptance in the register.

The direct reason for the change in this dog stud-book was a case in Holland in which a man I knew bred a litter of hybrids out of an Alsatian and a Giant Schnauzer (Bouvier), of which one male won for his new owner two first prizes as a Bouvier. This would have qualified the dog for full registration in the stud-book and I was able to convince my fellow-councillors that this was obviously absurd.

Chapter Twenty-Five

Selection for Production

Whereas in some of the domestic animals both sexes are equally valuable in regard to the direct use we can make of them, in about half the number of kinds of animals we fully utilize only one of the two sexes. In milk-cattle and laying-breeds of poultry, the females are of greater economic importance than the males.

In those animals where both sexes are of equal use, such as in horses or swine or fur animals, we have the great advantage that we can appraise the value of all our breeding animals; in milk-cattle and egg-producing poultry we are labouring under the handicap that we can directly evaluate the merits of one-half of the animals born only.

This does not mean that we can only judge the direct value of one-half of our animals, for all such animals are polygamous, so that we need to use only one male for several females, and if we make use of a good method of artificial insemination, this proportion is greatly extended. The drawback, that we cannot directly measure the egg-laying properties of our roosters or the milk-producing tendencies of our bulls, is not quite as great as appears on the surface. As we have seen elsewhere a system of selection, based upon the individual merits of our animals, falls far short of the ideal. The best breeding hen is not necessarily the hen that lays most eggs, and if, by any means, we could find out how good a layer a cock would have been with his particular inherited make-up, this would not be a sufficiently good basis for a system of selection anyhow. We might even defend the thesis, and with some hope of success, that the circumstance that we are able to judge a stallion as an individual performer tends to give too much value to those

individual qualities of that animal, so that in some respects it would be preferable if we could only judge his inherited make-up in a roundabout way, as in a bull, namely, by judging his offspring.

After all, the fact that we cannot directly see the effect of the inherited make-up in the qualities of the animal itself, when we are dealing with such animals as cows and goats, poultry and ducks, is a drawback, for if we could test the laying powers of a drake or the milking value of a bull, we could at least recognize the hopelessly bad ones.

It is evident that inherited factors play an important rôle in the quality of a hen as a layer, of a cow as a milk producer, and it is also evident that the father has as much influence upon the inherited make-up of the daughters as the mother has. This can be seen from the result of cross-breeding, for when the hybrids between two breeds have a certain quality in these respects we generally find that it does not matter whether the father or the mother belonged to the high-producing breed.

The idea that individual qualities are inherited as such has had its influence upon the breeding practices in these animals, for when in these matters we do not think in terms of inherited factors, which only indirectly help to determine the final qualities, but in terms of the valuable qualities themselves, it is easy to come to think that the rôle of the bull is to transmit his mother's qualities to his daughters. This idea seems to lie at the bottom of the system of judging a bull's quality as a father of good daughters, by looking at his mother's production record. It would not sound reasonable that breeders of milk-cattle would use all the tricks of their trade to bolster up the production record of a cow, if the buyers of a bull-calf from that cow did not have the notion that somehow this enormous production by the mother made the son a valuable producer of heifers.

The quality of a hen or a duck or a cow as a producer is only partly produced by the genes she carries in her cells, and again we must remember that even insofar as some of those genes help towards that good production, they are not necessarily transmitted to her daughters, for she may be impure (heterozygous) for many of them, so that only half of her daughters will obtain them.

No animal can be judged as a breeder of good stock by inspection of its personal appearance. There are two ways of judging a

breeder: we may judge the animal in its direct effect on the quality of its offspring, or we may judge its value for the breed to which it belongs. The real test we should apply to a breeder is whether it transmits useful inherited factors to all its offspring, and whether it does not transmit useless or harmful ones.

In theory we may picture a group of animals which is so pure that all the animals constituting the breed have an identical inherited make-up, being homozygous for all the favourable factors. In such a group selection of breeding stock is unnecessary, every healthy individual being as good a breeder as the next one. Such pure, wholly homozygous breeds of animals do exist, for instance in some of the laboratory animals, mice and rats. When the breed is not pure, however, and comprises a certain proportion of animals that are heterozygous for important inherited factors, it becomes necessary to find the individuals that are best from our standpoint, and to ensure that the majority of animals of the next generation shall be derived from these particular animals.

On paper this may seem a formidable undertaking, but in reality all it amounts to is the obvious statement that that animal proves to be the best breeder which gives the most profitable offspring.

It is evident that very often the animals with the best make-up will also be the best individuals, but this is not necessarily true, for an animal with a very favourable combination of hereditary factors may under the influence of adverse conditions be unable to show this good genotype by its individual excellence.

A stallion of a racing breed may, as a result of some accident in his youth, be quite useless at the track, whereas he may be an excellent breeder of fast young stock. A breeding hen of exceptional merit may herself be hatched so late in the season that the weight of her eggs and the number produced are very much below average.

Plant breeders nowadays know quite well how to distinguish between breeding value and individual merit. The most extreme example is that of the breeding of sugar-beet seed. To produce excellent seed economically, breeders of sugar-beets sow the seeds of their best families very thickly so that on a very small area they may produce thousands of "stecklinge", thin, weedy fingerlings. Those thin, scraggy beets have no economic

value as producers of sugar, but their inheritance is excellent, so that the seed they produce when they are planted out next season will be so good that it will yield a fine crop of excellent sugar-beets. Here the crowding of the beetlets destroys their individual value, but it does not affect their breeding value.

In selecting for economic production the only safe way is to select wholly for breeding results, and not for individual merits. The result in matters of breeding practice is that it is easier correctly to appraise males than females. As a cow generally produces only about two to four daughters, this group of offspring is too small to constitute a reliable sample of the sort of germ-cells she is able to produce. A bull, however, produces a considerable number of daughters, all from different mothers, every season, and it will be easy enough to evaluate him as a breeder of profitable stock.

For this reason it is easier, and also more important, to judge the males correctly by comparing the quality of their daughters than to get a clear picture of the breeding value of the females.

This is especially true of poultry, where several different things contribute to make it almost impossible to appraise individual hens as breeders. The date of hatching of a pullet has such a great influence upon her laying capacity that we can only compare those sets of daughters that have hatched simultaneously. This gives us about four daughters to every breeding hen, and this is exceedingly little by which to judge the mother.

It is true that the mother contributes as much to the inherited make-up of each daughter as the father does, and for this reason it seems impossible that any system of selection could be used which leaves the quality of the mothers out of consideration. Yet several breeders have tried basing their selection upon the testing of males exclusively with very good success.

This system would not work well if we had to base our choice upon the quality of just a few daughters of each father; but if we use sufficiently large groups of daughters, and take the precaution of equalizing the groups of mothers considered, as explained in the special chapters on cattle and poultry, we can safely assume that the best breeding male is the male that produced the best group of daughters.

In practice this means that in those animals we judge the value of a number of males by sampling their female progeny. Everything depends upon using adequate samples which have

not been modified as such by any selection. In cattle we can use the records of the first twenty daughters; in poultry we can use the records of all the daughters of a certain hatching date.

Using the actual economic value of the daughters as a criterion by which to compare the breeding value of the males used, we can never go very far wrong, for after all we keep those males in order to produce good daughters from them. Any other system of choosing males is highly speculative, and this is true both of the method of judging a male according to his mother or according to his own body points. In the selection of poultry the system of using large groups of daughters to judge the fathers by is especially valuable, as the birds are so fertile that we can discard the daughters of all but the one best father, so that in this way the animals from which we raise our next generation are all the descendants of a valuable proven breeder.

The greatest difficulty in any system of selection for high production lies in applying an adequate test to the animals. This is one of those instances in which we geneticists must help the breeders to set up adequate standards of perfection. At first sight it appears that in such animals as cattle and poultry, the goal we want to aim at is production. In reality we want profitable production. Our ultimate goal must be to produce a strain of animals that will give us an average profit per individual.

It is not necessarily true that the hen that lays the largest number of eggs of the greatest value is the most profitable hen. In a set of laying tests in Nymegen we found that hens vary so much in the economic utilization of food eaten, that two groups of hens that produce an equal lot of eggs of equal value may differ so much in food consumption that one lot is profitable whereas the second group is kept at a loss. The same is true of cows. Up to a certain point the higher the food consumption, the greater the profit from the milk produced, but after all the only body-character that is correlated with yield is size. The larger cows produce *more milk* than the small ones; but this does not mean that the larger cows produce *cheaper milk* than the smaller ones. It would be the height of folly to select for production only, as this might very well result in a gradual increase of body weight, and in a decrease in the economic production of milk.

It is quite possible that under our present system of apprais-ing the value of our animals in productive strains, selection for

production only, without regard to profit, pays better than striving for economic production. In poultry our present laying tests call for hens that produce a great number of large eggs, no matter how much food they consume. It seems almost unbelievable that at the tests the most profitable groups of hens are not necessarily the prizewinners, but for so long as this is true, a breeder who breeds to sell, rather than to produce his own egg-layers, would not be justified in giving too much attention to profitable production. The thing which we must change is the system of laying tests, and we must change it until the groups of hens that produce eggs most cheaply, the best hens, really are able to show their superiority.*

Economic production is the result of a great many factors that co-operate. Both in cattle and in poultry those factors are essentially the same. The most important of them are, firstly, early maturity, which reduces the unproductive period before production starts; secondly, good production, both quantitative and qualitative; thirdly, economic food-consumption; fourthly, longevity.

Danish production tests have conclusively shown that the cows that live to the greatest age produce milk for the lowest price per gallon. The same is true of hens, with which the cost of replacement of each producer is relatively high.

In former times, much money was lost by basing the value of breeding stock of productive breeds on false standards. The idea that the breeding value of an animal can be recognized by a simple inspection of its conformation has done harm.

* I think the poultry industry is beginning to realize this now (1953).

(See illustrations between pages 180 and 181.)

FIG. 29.—Graph showing the progeny of one cock in respect to egg production. On every horizontal line a hen and her daughters are arranged, the mother in a heavily ruled square. As can be seen from this table, some hens have given better daughters than others, but there is very little relation between the number of eggs laid by a mother and the average quality of her group of daughters.

Konsulent Davidsen kindly made this photo for the author from a wall-chart shown at the International Agricultural Show in Kopenhagen, 1938. It is reproduced by courtesy of Statens Aegudvalg, Denmark.

FIG. 30.—The progeny of one cock and eleven hens in respect to egg-weight. The mothers are enclosed by heavy squares, and the daughters of each mother are grouped on the same horizontal line as the mother. Some mothers have better daughters than others, but it is impossible to prophesy the egg-weight of the daughters from the weight of a hen's eggs. The daughters of this male average higher than the mothers.

Photo made by Konsulent Davidsen from a wall-chart shown by the Danish State Poultry Selection Institute, at the 1938 Agricultural Show in Kopenhagen.

NOTES

"No animal can be judged as a breeder of good stock by inspection of its personal appearance."

"The real test we should apply to a breeder is whether it transmits useful inherited factors to all its offspring, and whether it does not transmit useless or harmful ones."

In these two sentences Hagedoorn sums up the main thesis of his book. Were their message accepted universally there would, undoubtedly, be an improvement in the productivity and profitability of the world's livestock. Not perhaps, such a rapid advance as Hagedoorn presumed, because productivity is in practice limited by environment, especially by nutrition, rather than by breeding, and because profitability in farming nowadays depends rather more upon what money and Governments are doing than upon what farmers are attempting to do. Nevertheless, so far as the breeding factor in animal production is concerned, Hagedoorn's thesis is incontestable.

The greatest practical difficulty is to design tests which give reliable measure of breeding merit. As Hagedoorn says:

"The greatest difficulty in any system of selection for high production lies in applying an adequate test to the animals."

Many of the tests on which selection for production are at present based are, in fact, very far from being reliable. Hagedoorn himself cites several instances of such imperfection, for instance, the absence of figures for food consumption and food conversion in conventional methods of milk or egg recording. Particularly where records of performance are used—as they are frequently used—as advertisements in the sale of breeding stock, so far as genuine livestock improvement is concerned, incomplete records of this nature might in the end prove rather worse than none at all.

Chapter Twenty-Six

Tests and Trials

The only really effective test of quality in a breed of animals is the judgment actual use will produce in time. It is never possible to proclaim either a breed or an individual good or bad, unless we take into account the object we have in using it. In many breeds it is impossible to test the quality of a great many individuals, namely of those of one sex, where only individuals of the other sex are used.

In certain instances it is possible to judge of the quality of an individual by just inspecting it. This is true where we keep the animal solely to look at, such as in show pigeons, goldfish, many rabbits. The influence of the shows has been to substitute inspection of individuals for real tests of value, and we have seen that even in economically important animals the shows have obtained an importance out of all proportion to their reasonable value.

Where the animal is not only valued for its looks, as with animals bred purely for show purposes, it has often been deemed advisable to institute some sort of a test, destined to measure the performance of the animals. One of the most obvious tests is the progeny-test, which measures the animal's performance as a breeder, and to the progeny-test is devoted a separate chapter.

It is evident that when we keep a breed of animals for a certain purpose, testing the actual performance is better than just looking at the animal and guessing how much its appearance tells us about its probable performance. On the other hand, few tests are perfect, and some have grave faults which make them almost useless. Most tests are not really instituted by independent persons interested in the relative merits of a

number of competing animals, but by owners anxious to demonstrate the quality of their animals.

One of the oldest and best-known examples of animal testing is horse-racing. This is a very good typical example. Everybody knows that in racing the horses entered are not compared in order to find out which of them has most endurance and greatest speed, but which of them shall win this particular race. The saddling, the training, the weight of the riders, the condition of the track, everything is adjusted to this particular purpose, so that nowadays nobody thinks of horse-racing as a method of finding out which is the best riding horse for fast work.

A very good example that shows how a test can deviate from its obvious objective is that of the poultry laying tests.

When the first full-year laying tests were started in New South Wales, the object was to determine which breeds of poultry were most superior for the purpose of egg-laying. Later the tests were mainly used to show the relative merit of different strains of birds within a breed.

From the outset up to about twenty-five years ago the only quality measured was the number of eggs laid. Very soon were found birds that laid over 300 eggs in the first year, and strains of birds producing well over 250. It was soon found that the size of the eggs should not be neglected, for some of the 300-egg birds were hens of great size that produce a small egg every day and could easily keep this up almost indefinitely. However, the production of many large eggs by half a dozen hens entered in the contest by one breeder does not show that this breeder sells nothing but very profitable poultry. I have made quite a lot of study of laying-test results and methods, and have consequently made myself very unpopular with many authorities and breeders.

Two points were overlooked at the outset. In the first place, it is possible for a smart breeder to enter a pen of test birds that will lay very many heavy eggs, while the general run of stock sold by him does not come up to this standard of excellence at all. The breeder can set aside some proven breeding stock for producing laying-test winners: he may even buy his test pens. England is not the only country where such pens are for sale to prospective competitors at the laying tests.

In the second place some hens in producing eggs utilize their food much more economically than others. In the end it is not

the production of many heavy eggs that counts in keeping poultry, but the economical production of eggs.

The first point can be taken care of by ensuring that the groups of test birds constitute real random samples of the birds at the competing farms. This can be done in different ways, one of the simplest being to take large samples of hatching eggs, in the way I indicated at the Ottawa Poultry Congress, 1927, and which was first adopted in England at the Norfolk egg-laying trials in 1937.

Around 1925, I got the German poultry-breeding officials interested in the fact that food consumption as well as egg production should be registered at the tests. All the official German tests now classify the groups according to the difference between the value of eggs produced and the cost of food consumed. Tests run by the Dutch Genetical Society in Nymegen have shown that food consumption is so important that results are wholly fictitious when it is not taken into account.

Greyhound-racing, like horse-racing, is a spectacle and an occasion for betting rather than a test of the value of greyhounds for hunting. Racing homing pigeons is perhaps one of the most reliable tests for real value in performance, as here nothing but speed and an infallible homing instinct count.

Sheep-dog trials are very interesting in a different respect, firstly as a test of obedience and intelligence, secondly because they show how breeding for show purposes ruins a good breed for practical purposes. Collies of the show type have a poor chance of winning such trials in competition with the real sheep-dogs.

The testing of police-dogs has become a farce in some countries, where the ability to learn the tricks prescribed and to perform the actions deemed valuable, has been exaggerated in importance to a very great extent.

Field trials for setters, pointers and coonhounds are much more useful to find the right sort of dogs, but to a certain extent they have the same fault in common with any other trials of dogs, namely, that they do not measure resistance to fatigue, one of the most important qualities of all.

Cock-fighting, although formally prohibited, has been reviving. In cock-fighting chance enters to such a large extent that it is hardly more than a fine excuse for gambling. Much more effective are the crowing contests one sees in some parts of

Germany. At these contests one witnesses a crowd of extremely serious fanciers, timing the number of times the competing cocks crow within an hour. Here training and feeding enter into success, but the most important factor deciding such bloodless competitions is the inherited quality of the cocks of this special breed of songsters!

The same can be said for the extremely long-winded contests between groups of performing pigeons, tipplers and rollers.

Endurance tests of riding horses are extremely useful. In the first place they show the superiority of certain breeds over others, and, secondly, they indicate differences between individuals. Tests for draught horses, in which dynamometers or braked vehicles are used to measure the force of individuals, have not been very popular so far, chiefly, I think, because they tend to demonstrate that show type has no connexion with real utility-value, so that breeders and exhibitors have so far looked askance at this novelty.

In swine, feeding tests have been rather useful to demonstrate the superiority of certain breeds and first-generation hybrids in respect to utilization of food in putting on weight. These tests are mostly run as progeny-tests. They are far from perfect, in that generally only four pigs out of a litter are tested, so that the important question whether the parents are homozygous or carry unpleasant recessives is not decided.

In dairy cattle milk-testing is very important. The most complete test is that in which all the milk is weighed, and frequent samples are tested for fat content. A sampling test in which the inspector milks the animals at intervals of two or three weeks, is often substituted, and at times, if not very often, where the inspector's visit can be anticipated, this gives rise to some trickery or downright fraud.

Milk-testing is incomplete when the weight or size of the animal is not taken into account. Food conversion is as important as milk production in finding the value of a dairy cow. The first country in which this was sufficiently understood was Denmark. The really important point in milk production is the cost of milk per gallon. As large cows as a group give more milk than small cows, but as one unit of area supports more small cows than large ones, this amounts to saying that the important point is the production of milk per acre, just as in sugar-beets sugar per acre is more important than sugar per beet.

It is certain that, where the pasture is first class, large cows produce milk more economically than small ones, if the size does not go above a certain maximum; but there certainly are farms where smaller cows give more milk per acre than large ones.

Measuring milk production only in gallons of milk per cow per year is as ridiculous as measuring sugar production as sugar per beet. The best dairy cow is the one that is able to transform the products of the farm into milk in the most economic way.

I have not tried to be exhaustive in this chapter; it has been my aim to give a general idea of different ways of testing animals in regard to performance, and to indicate the difficulties inherent in this work.

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The general conclusion to be drawn from this chapter is that while the testing of farm animals in regard to performance is highly desirable it is, nevertheless, a task of greatest difficulty. As Hagedoorn demonstrates, most testing methods are incomplete, some are fallacious and, when competitive, subject to complete misrepresentation or even to fraud. It would be well if all geneticists were better aware of these possibilities which Hagedoorn with his wider experience so clearly recognized.

Chapter Twenty-Seven

Progeny-testing

It is really very curious to see how slowly the importance of progeny-testing is recognized. It seems obvious that as the only real object of a bull is to produce offspring, the only really important question to ask when buying a bull or using one is whether he is likely to produce good calves. The only safe way to answer that question is to see how he has bred.

It is evident that the users of live stock, the farmers, are fully convinced that the way a bull or a boar breeds is the only really efficient way to test his worth. Why then are our authorities on animal breeding so slow in taking to the idea?

The answer lies in the fact that the influence of the cattle shows has taught us to regard the individual rather than the breed, the animal rather than the way it breeds.

In the days of Bakewell and his colleagues the idea of leasing out young bulls and young rams in order to test their value as breeders was not new. Since that time, however, we have seen the cattle shows blossom out, and assume an importance that has for a time overshadowed every reasonable consideration in animal breeding.

When we geneticists began to interest ourselves in applied genetics, most of us were botanists. Only a very few of my colleagues have interested themselves in animal breeding, and this is not to be wondered at when we consider that a geneticist can do a lot of very useful work in the amelioration of plants, which work is generally concentrated in experiment stations and seed firms, whereas it is very hard work for a geneticist to get the confidence of the animal breeders.

The curious fact exists that after the coming of genetics, the

idea of judging a breeding animal according to the way in which it is successful as a producer of young stock had to be rediscovered. I am not generally much of a stickler for priority claims, but on this one subject I would like to translate into English what I wrote in the first Dutch edition of my animal-breeding book. In 1912 I wrote:

"The only way to judge the quality of a bull in a breed, in which fat content of the milk is of great value, is according to the fat content of the milk of all his daughters. And we know that it is important to see to it that in reality all his daughters are examined."

About 1925 many geneticists started to become interested in "bull-testing", and many different systems have been advanced by which the breeding value of sires can be measured.

Most systems of progeny-testing can be classified into two kinds. Some authors take into account the quality of the females used for mating, and use daughter-dam comparisons for judging the sire; a few others prefer to leave the dams out of consideration. At first sight it seems obvious that a bull, whose daughters average better than their dams, must be superior as a sire as compared with a second bull, whose daughters are not as good as their dams, even if the average quality of the two sets of daughters is alike. Most bull-indexes for this reason take into account the quality of the dams, by rating the quality of the daughters as midway between that of the dams and of the sire; sometimes, as in the first Mount Hope index, with complications derived from considerations of dominance of separate genes.

The more I have studied the subject, however, the more I am convinced that the best test of the breeding value of a sire is the average quality of his daughters, when unselected groups of daughters are taken. In the first place, the object of studying the results from breeding a given sire is to get an idea of what the quality of the sire's daughters is likely to be in future. When we know a bull has produced a lot of daughters that yield milk containing 4 per cent. of fat, we can be sure that the daughters he will produce in future from the same sort of female stock will be of that same quality. When we state that a bull has produced so many daughters with this quality we state a fact. When, however, we confer an index on him based upon a comparison of the daughters with the dams, we leave the facts and state a hypothesis.

In animal breeding we have had too few facts and too many theories. The theory that it was possible to judge of a bull's breeding value by looking at his back, the set of his tail and so on has done quite a lot of harm. The theory that it would be possible to judge a bull by the yield of his mother has been proved untrue. I hesitate to advocate another plausible theory as a substitute for those that have been proved untenable.

We must remember that the milk yield of a number of cows is due to two different things, to the inherited make-up of the cows, and to the way they are managed. The average quality of a number of heifers gives a much better picture of the genotype of this group, than the average quality of a group of dams gives of the quality of that older group. This is evident to anybody conversant with milk-testing in highly-bred cattle. Promising cows are given special treatment to bolster up their yield, when records become of special sale value.

The dams with which a promising young bull is mated are certain to be a selected group, if only for the reason that disappointing heifers are weeded out of all herds. A bull-index based partly upon such figures is sure to give a somewhat distorted picture of the bull's breeding value.

It is very important that the group of daughters according to which a bull is rated should represent a sample of his female progeny. If it is impossible to examine all the daughters of a bull, a random sample should nevertheless be examined, for instance the ten or twenty first-born daughters. It is very important that no female offspring shall be omitted. The statement of a bull's breeding value should state the number of female calves born, the number raised, the number discarded, the number of days milked of every heifer, and the results.

For obvious reasons the first lactation period of a bull's daughters is more correct to use as a measure of his transmitting ability than subsequent milkings of the same daughters.

The use of more complicated bull-indexes, especially those in which the bull's value is measured by adding or subtracting the difference between dams and daughters to the daughter's yield, needlessly handicaps the record of a bull used in herds of selected cows. In herds where only very high producers are kept, the average yield of the dams is not a fair measure of the genotypic quality of those dams, and a very good bull bred to such cows may have an indifferently good index, when the

average quality of his daughters is weighted by correcting it as a test of the bull's ability by subtracting the difference between the daughter's and the dam's record.

The average yield of a herd of cows, often assembled from different places, in which the yield is sometimes raised by the rejection of poor producers and sometimes not, but always apt to be modified by special care, is not a figure that should be used in weighting the quality of a set of daughters of a bull. The daughters of a bull have this one father as a common factor affecting their quality. If sufficient care is taken that a group of daughters is a random sample of what a male can do, the average quality of such a group is a very good measure of the sire's quality.

The use of the complicated indexes has one great drawback, it will lead to all sorts of tricks to bolster up the indexes of young bulls, when once bull-testing comes to be appreciated.

Let us take the case of a bull whose daughters have an average yield of 1,200 gallons. The cows he has been mated with are of two kinds, good ones, averaging 1,500 gallons, and poor ones, averaging 900 gallons. If we would rate the bull according to the quality of the daughters from the good cows, his index would be 900 gallons, but if we rate him according to the daughters from the poor cows, his index would stand at 1,500 gallons.

When the same bull has been siring calves in two herds of cows with a different yield, the average quality of his daughters generally differs very little. Everything considered together, I am greatly in favour of rating a bull according to the average quality of a random sample of daughters, rather than according to some complicated index.

Selecting bulls according to progeny tests is still rather a novelty, excepting in Denmark. In other animals, however, selection by means of progeny tests has been in operation during many generations, and the results have been so good that we can now recommend this method from actual experience.

In poultry, both in hens and ducks, selection of layers used to be based on the individual laying records of good females. It used to be recommended to select the very best layers for a breeding pen, and to mate such groups to the son of the very best mother (R.O.P.). Results have been remarkably disappointing. Ten years of strict selection for heavy egg yield of

Plymouth Rocks at Maine Experiment Station was wholly inefficient in raising the average egg yield (R. Pearl, 1908).

We now know that several non-genetic factors have more influence upon the number of eggs laid by a pullet than her genotype, the date of birth being among the most important influences. When we set apart a number of hens, that have laid the largest number of eggs, we have no reason to believe that these hens on the average have a better genotype than the average flock from which we selected them. The common experience of egg-farmers is that the daughters of exceptionally good hens are disappointing, whereas the daughters of poor hens are surprisingly good. This simply means that the good or poor quality of a hen depends to a great extent on non-inherited factors.

In theory there would be two ways of using progeny tests in poultry-breeding. We could test hens as well as males as parents.

In this way it is very easy to find out which group of pullets has been the most profitable one. This obviously is the group bred from the best father. When the breeding season comes round, these pullets of this best group are used as breeding stock to raise the next generation. They are mated with half-brothers, cockerels from the same breeding. This necessitates keeping a sufficient number of cockerels alive from each father, of course, until the breeding season.

This system looks complicated on paper, but it is very much simpler than the most common system of basing selection upon individual laying quality of hens. It means in-breeding, but only to a mild extent, and at a pinch a man can keep the progeny of the two best males and mate the daughters of one to the sons of the other and vice versa. As I have explained in the chapter on in-breeding, the danger of in-breeding lies in overlooking important points, because our attention has been distracted by other obviously important ones. In my system of progeny testing poultry and of selection in the male line, this is obviated, when the basis of selection is actual profit in different competing daughter-groups.

Several breeders have been using my system for a number of generations, with very great success. The most striking results have been obtained with Khaki Campbell ducks. On one farm it has been possible to raise the farm average from 225 eggs

per duck to just over 300 per duck per year by means of this system. (Ten years later this figure was 340.)

Compared with the usual system of basing the selection of males upon the mother's egg record, my system differs in the circumstance that there is no chance of picking a poor male with a good mother as a breeder. Whether a male shall or shall not be used to continue the breed depends wholly upon the average quality of his progeny. In the beginning it frequently happens that a few males disappoint, but such males have no chance of influencing the following generations as they are discarded with *all* their progeny.

In the breeding of swine, progeny-testing is used extensively in Denmark. Sows are so fertile that here the work can be done both with females and males: but as in all polygamous animals, the rapid progress is due to progeny-testing males. A very important point in all animals, including pigs, is that the lot of descendants according to which a sire is judged, shall be a real random sample. When it is possible for the breeders to make a few young animals disappear, the value of the progeny test becomes problematical.

In swine, as in most other animals, we aim to get uniformity, and this means homozygosity. For this reason we want to recognize the sires that give no aberrant offspring. In swine heterozygosity for important inherited factors is rather common, many males producing piglets with hernia, with aberrant feet or blind gut, or dwarfs. A system of progeny-testing that makes it possible that boars, heterozygous for such factors, come to be known as famous sires, fails in its object.

Fattening tests and growth tests in swine, in which four pigs of each litter are tested on gain per unit of feed, and suitability for slaughtering, have the very great drawback of allowing of this possibility. It has been urged that in selection we have to progress step by step, and that the eradication of lethal factors will be taken care of when the right type of hog is once fixed, but this reasoning is genetically unsound. In selection everything that affects economic usefulness must be taken care of at the same time, for only in this way can we obviate the possible necessity of ever having to abandon the purity and fixity attained with so much trouble, because some neglected fault has been bred into the strain. When in selecting such animals as swine we allow the breeders to hush up the birth of weaklings or

malformed piglets, we stick our heads into the sand and build up lots of easily avoidable trouble for the future.

There is no reason, with animals in which reproduction is so rapid as in swine, to allow any of the boars to continue breeding if they give good, bad and indifferent offspring. Only those in which all offspring are faultless and of the correct type should be used for the breeding of the males of future generations.

In different countries systems of selection have been proposed for swine, using progeny-testing in certain ways, but often, as stated above, in a half-hearted way. Although we geneticists ought to be glad that rational tendencies in animal breeding are gradually being substituted for irrational methods, it is wise to point out that the danger exists, that the name of progeny-testing or bull-testing is used for methods that are only *half-way* efficient.

A bull, ten highly-productive daughters of which are known, cannot be said to be a tested bull in the sense we wish that term to be used, i.e. for animals whose probable homozygosity for important genes is proved by the high quality and low variability of a random sample of their offspring.

One of the first requirements for progeny-testing is registration. There is no way of showing that a sire averages very good offspring unless we can discover his descendants.

At first sight it appears as if the herd-books will come in extremely useful in this respect; but as most herd-books have not been established to make progeny-testing possible, they often have certain faults that make their use very difficult. In the first place, some herd-books do not register all the animals of the breed, not even all the pure-breds. The Continental herd-books generally have a preliminary register, in which births are registered, and a herd-book in which only those animals can be registered that pass an inspection on show points.

This selective registration precludes finding all the daughters of a bull, or all the piglets a boar produces.

The second difficulty is perhaps even more serious. In most herd-books the names and numbers of all the registered animals born during one year are published, and in each animal sire and dam are given. This makes it very easy to construct the pedigree of any given animal; all we have to do to fill out a

pedigree is to work back from parents to grandparents, from grandparents to great-grandparents and so on.

When we want to work in the other direction, when we want to find out, as regards a stallion or a bull, which registered animals have been sired by him, we are up against it in some herd-books! Very often the administration does not allow of doing this work efficiently. When a few years ago a young man in Holland wanted to study the way in which show points in bulls were correlated with show points in daughters, and for this reason simply wanted to find all the daughters of seven famous bulls, the herd-book authorities who had registered those bulls and his daughters told him that a system by which those daughters could be traced did not exist. He therefore had to look through the printed herd-books of several years, page by page, to find all the daughters of those bulls, a painstaking labour which took him most of his vacation! I am glad to say that both large cattle herd-books in Holland now have a card index, in which the registered progeny of a bull can be found at a glance. This is what every herd-book should have, but what as a matter of fact very few of them have.

Both difficulties, the non-registration of aberrant or less beautiful animals, and methods of registration that make finding the descendants of a given animal almost impossible, arise out of the two principles of the old-fashioned herd-book systems, namely, the idea that the characters of an animal are inherited by its descendants, so that an imposing pedigree in which nothing but first-class animals are found not only helps to sell a young animal but actually proves its value as a breeder.

Most people breeding horses and cattle were so used to the fact that buying a stud is a gamble, that they hardly thought it worth while to find out whether the famous names in the pedigrees stood for prepotent sires or for erratic breeders.

Prepotency as such is not inherited from father to son, for prepotency from a genetic standpoint spells homozygosity. A sire, homozygous for a great many economically very important inherited factors, will produce very many good young stock, but when mated with a female heterozygous for an important factor, he may well have a son or a daughter who inherits that factor only from him, and therefore is heterozygous for it. Even

if for this reason, however, we know that prepotency as such is not inherited, yet the importance of homozygosity (prepotency) goes further than its importance in respect to the generation of direct descendants. In a polygamous animal-group, the use of many homozygous sires has an important influence upon the proportion of homozygotes to heterozygotes, and so upon the percentage of aberrant, comparatively less valuable offspring in the breed.

The ideal system of breeding in the larger animals is extensive progeny-testing, combined with artificial insemination of the greatest number of females with the sperm of the sires that have been proven prepotent and with the elimination of the descendants of unproven or unworthy sires.

In Holland both herd-books have established a system that goes in the right direction. Some bulls are declared "preferent". The first step in this process is taken by the owner of the bull who asks for the animal to be investigated. When this request is granted, a committee visits the district where the bull has served, and examines his descendants and their records. The system would be excellent if it were done early enough in the life of the bulls, and as a matter of routine as regards most apparently good bulls, and if most of the attention were given to the economically most valuable points.

In discussing the work of the herd-books, we must never forget, if we want to be fair, that a herd-book association is a society of breeders of a special type, namely, breeders who make money from the sale of good-looking breeding stock. Registration in those herd-books is highly selective, and the selection is mainly on show points and points believed to show "constitution". The result is that in passing judgment upon a bull that is proposed for a declaration of "preference", show points in his offspring have the first consideration of the committee. The final summary reports upon the body-conformation of the daughters, the average shape of their horns, backs, tails, legs, udders, and so on. The show points and attractive appearance of the sons are not forgotten, the fact that many bull-calves are raised from among his offspring is decidedly in his favour. Finally, the milk production of the daughters and the fat content of their milk are discussed, but these points are in no way the most important ones. Sometimes a fine bull with a lot of beautiful sons and daughters is declared preferent, when the

committee has said that the yield of the daughters has been sufficiently good, or "not unsatisfactory", very faint praise in a dairy breed. There have been periods in which almost no bulls that were still alive were thought worthy of the predicate; about twenty years ago there was only one living preferent bull in the county of Friesland, the district in which one of the herd-books operates.

The present system is widely criticized. I have seen these bulls called "Holland's architectural masterpieces" in a South African periodical, and I have repeatedly written on the subject myself. This system nevertheless has its excellent points, and could easily be improved into a worth-while system of bull testing. Milk production should be given more importance; it should count for 80 to 90 per cent. in the final decision, not for 20 to 30 per cent. The new card systems, which allow of finding all the daughters of a bull quickly, should make this sort of testing more easy and rapid; it could be done first in the office of the herd-book on figures only, and afterwards all bulls having highly-productive daughters could be examined in respect to prepotency for show points. One of the greatest drawbacks of the present system is that it makes it appear that only a small minority of bulls in Holland are worth anything as breeders, whereas probably the great majority of them are prepotent for factors necessary for economic milk production. Especially should an improved system be worked as early as possible in the life of a sire in order to make it possible to use him for breeding.

Some herd-books have adopted an imposing-looking system of graphically representing correlation between dams and daughters in respect to milk yield and fat content. By a system of quasi-genetic juggling, in which it is necessary to use three different unproved assumptions (which all have this in common, that each is extremely improbable!), the genotype in regard to "the" five genes for fat or for milk is "easily" found for each sire. I do not think we geneticists ought to be too lenient in criticizing this sort of pseudo-genetic humbug, which is very likely to discredit our science in the eyes of intelligent breeders. The German author von Patow is responsible for this invention.

The stunt of showing a sire with half a dozen beautiful children has become rather popular at horse shows and cattle

shows. It need hardly be said that such exhibitions have only advertising value. As the group is far from constituting a random sample of the sire's progeny, the system has nothing to do with progeny-testing in a practical and real sense.

NOTES

This chapter, to my mind, is one of the best and most valuable in all Hagedoorn's book. He begins with what I regard as a classical statement of the common-sense basis of progeny-testing.

"It seems obvious that as the only real object of a bull is to produce offspring, the only really important question to ask when buying a bull or using one is whether he is likely to produce good calves. The only safe way to answer that question is to see how he has bred."

The logic of this statement is incontrovertible. In practice the advice is rather more difficult to follow. Were a dairy farmer determined when going to market only to buy an old and proven bull, he might come home empty-handed or with a bull which for some reason or another was no longer attractive to its owner. Most bulls for sale are young bulls and therefore it is in all probability a young bull that the dairy farmer will buy. The progeny-testing will have to wait until the bull has come home. That, of course, is why bull-buying is and always has been a gamble. By study of pedigree, of records, of herds, contemporary relatives and the bull's own phenotype the bull-buyer does his best to increase his chances of a successful gamble. Yet it remains a gamble, and genetics, which in its modern form is so largely a mathematical exercise in random distribution, has done little to eliminate that element of chance.

With the development of A.I. and the accepted target of no more than 200 bulls serving some 2,000,000 cows, the possibility, in addition to the advisability, of progeny-testing has vastly increased. Obviously no bull should be permitted to stand at an inseminating station until it has been seen "how he has bred". It would be a further safeguard were he mated with his own female progeny—one form of test-mating—as well as progeny tested. After all, with A.I. and its deep-freeze extension there is no need, it might be said there is no excuse, for using a bull widely until the most hidden recesses of his genotype have been thoroughly explored.

After reiterating his criticism of the futility of show-yard standards, with which most people not concerned in that specialized activity are now generally agreed, Hagedoorn goes on to another matter which deserves a great deal more attention than is being given to it at the present time in that, as Hagedoorn puts it: ". . . the name of progeny-testing or bull-testing is used for methods that are only half-way *efficient." Such criticism is, in my view, particularly applicable to the system of progeny-testing of boars being so extensively and expensively*

adopted in this country at the present time. Sires should, if progeny-testing is to be any real advance on older methods, be tested on a random *sample of their progeny, and yet in fact this is not being done. As Hagedoorn puts it:*

"When it is possible for the breeders to make a few young animals disappear, the value of the progeny test becomes problematical."

"Fattening tests and growth tests in swine, in which four pigs of each litter are tested on gain per unit of feed, and suitability for slaughtering, have the very great drawback of allowing of this possibility."

Chapter Twenty-Eight

Progeny-testing the Females

During the second world war, when I was cut off from intercourse with my American and English colleagues, animal breeders and animal-breeding authorities became progeny-test-conscious. Progeny-testing has ceased to be a novelty, and better methods of evaluating breeding stock have come to stay.

During recent years, wherever I have lectured, as well as in connexion with my correspondence with breeders of all sorts of livestock, it has been necessary to discuss how far it is feasible to ameliorate the quality of livestock by progeny-testing the females as well as the males. This problem is of the utmost importance for the breeding of milch cattle as well as for sheep and for poultry.

It is evident that in these three classes of livestock, judging the males according to the way they breed instead of according to their personal qualities has so many advantages that serious breeders all over the world are now convinced that progeny-testing those males is indispensable. It seems obvious that if this method will help us find the best males, it would also help us to find the very best individual females. After all, at least in cattle and poultry, the females are the most important individuals—we keep them to exploit them. For this reason it seems absurd to many breeders that we should advocate the concentration of all our attention upon the males. Whenever the nucleus system of breeding is criticized, the main objection is almost always that as the females are so much more important, it is they who should be considered in the first place, rather than the males.

Breeders who now have some practical experience of progeny-testing methods know that in comparing the progeny of a

number of males, the one thing we base our judgment on is the quality of the females, the milk yield of the heifers, the wool production of the flock, the egg production of groups of pullets. Even if it is realized that the males statistically are more important than the females, we base our judgment of those males not on their own quality as individuals, not on their phenotype, but on their hereditary make-up, on their genotype. It is quite possible to abolish the score cards of bulls entirely (in fact, the Ayrshire Breed Society in the U.S.A. has done just that) and give all our attention to the female relatives, to female ancestors and female progeny of those bulls, even when we want type as well as production.

To test the quality of the progeny of one male, the most obvious method would be to consider that progeny group as such, and to find out its value for the particular purpose for which the breed is kept. In poultry this is exactly what we are doing if we can house the daughter groups separately, in folds or laying cabins. In many instances, however, especially with cattle and with poultry and sheep, this is sometimes technically impossible. Poultry are often kept in very large groups, the daughters of several fathers living in one large laying-house: and it is seldom possible to keep those small progeny groups separate in sheep. With dairy cattle, too, the daughters of one father may graze in company with many other beasts. In all these instances, individual records are obtained by special methods—with hens we resort to trap-nests, with cattle to milk-testing methods, and with sheep we keep individual records of the quality of progeny groups at shearing-time.

This means that in a large group of daughters by one father, we find good animals, mediocre ones and decidedly bad individuals. How should we utilize those individual records in our selection programme?

One of the first results of obtaining all those data on individuals is the possibility of judging whether the particular male who sired the group was heterozygous for many important genes. Each male, to give us a group of daughters, was mated to quite a number of females, especially with cattle and sheep; but even with poultry a breeding pen will almost always consist of ten to twenty hens. In the beginning some of those females must be heterozygous for important genes. For this reason the universal high quality of a progeny group from one male mated

to a great many females shows that father to be homozygous for many important genes in respect to which some other males are not. We must remember that this does not presuppose that we know any of those genes separately. In fact, we should never confuse progeny-testing with gene-analysis. It is relatively unimportant that we should learn to know those important genes as such, if we are out to purify a good breed, for the danger always exists of over-emphasizing the value of a gene we do happen to know.

What we are really after in progeny-testing our animals is to find the individuals that are homozygous, in all those difficult cases where complete dominance prevents the recognition of heterozygotes by inspection of individual quality. As long as we cannot apply a direct test-mating with the corresponding recessive, our only hope of distinguishing the homozygotes is mating them to a number of mates, so as to make sure of at least a few heterozygous ones.

Let us, as an example, consider the case in which we are dealing with just one gene. Let us suppose that *Aa* animals are indistinguishable from homozygous *AA* ones. If we mate a bull (or a cock or ram) to ten females and four of these happen to be heterozygous, *Aa*, there will be some recessives, *aa*, among the offspring when the male to be tested was *Aa*. On the other hand, if all the offspring show the presence of *A*, this makes it very probable that the male tested was homozygous, *AA*. A good example is polledness in Redpoll cattle, rose comb in Wyandottes, white colour in Merino sheep (as contrasted with black). In other words, if we examine the progeny of one male and ten to twenty females, we have a very good idea about the purity of that male for important genetic factors.

It is, however, equally clear that mating such a male to just one or two females would not give us the required data. To take the same example: we mate a polled bull to one cow, or a rose-comb Wyandotte to one hen. If that one mate happens to be a homozygote, *AA*, all the offspring will show *A*, whether the male tested was homozygous or heterozygous (*AA* or *Aa*). This is important, for if we raised twenty chicks from that one mating in our Wyandottes, they would all have rose combs even if the father was heterozygous.

To resume, when we are handicapped in our selection by complete dominance, we can test-mate or progeny-test males

by mating them to a sufficiently large group of females, and the results will be good as long as that group of females comprises some that happen to be heterozygous for the genes in respect to which we want to test that father.

One single mating, no matter how large the group of offspring raised from this combination of two animals, will never give us a satisfactory answer. This is just why the test-mating of a female is so very difficult. If a female should be heterozygous for some important gene, we would never recognize her as impure, unless we happened to mate her to an equally heterozygous male and raised a sufficiently great number of offspring from that mating. In other words, in such very fertile birds as poultry it would only be possible to test-mate (progeny-test) a female by mating her to ten or to a dozen different males. This means that the examination of the progeny of one single female gives us no insight into her breeding quality. If her offspring are good, this may be due to her mate.

Here lies the enormous difference between progeny-testing males and progeny-testing females. In the males, hidden impurities (and this is really what the progeny-test is for) will make themselves felt, through the birth of inferior offspring from some of the many matings. In the females, however, where every individual is only mated to one or two males, the chance of a really crucial mating (with a heterozygote) is very much smaller, and it will become smaller and smaller when the group becomes more homogeneous and purer.

A hen that has given six excellent daughters may be a good breeder, but this excellent result may equally well depend upon the genotype of her one mate. In a cock, however, that has been giving daughters from a dozen mates, the absence of culls shows him to be pure in respect to all sorts of valuable genes.

Records of production of individual ewes, milk records and breeding records of individual cows, and trap-nest records on production and fertility in hens are of great importance. We must, however, realize that individual records of such females tell us no more than what the constitution of those few animals is. In many instances cross-bred females show excellent records —they are regular breeders, good producers, and when mated to a pure-bred sire they may even have excellent daughters.

The real object of progeny-testing as a method in animal breeding is certainly not only to pick out a few valuable,

homozygous breeders (in the male sex): it should be to purify the breed, so that future generations of animals in the breed will be more certain to be profitable for agriculture.

If it were really possible to test both males and females, our object would be sooner approximated. It is regrettable that, with the possible exception of pigs (where each female can produce many offspring by half a dozen different males), there is no adequate method of progeny-testing the females. When the breeders of poultry, cattle and sheep continue to pay a great amount of attention to the quality of those females, they are absolutely right, for the evaluation of the female stock must give them the data by which to judge their male breeding-stock. For obvious reasons the breeders tend to believe that selection in the female line is of the greatest value. Even breeders who are using progeny-testing methods to select their males will be convinced that selection in the female line is of still more importance. They seldom stop to consider that what they are judging in the females is phenotype, individual quality, and not genotype—breeding value.

Now, what is the result if we rely upon progeny-tests of our males entirely and if we stop selecting females? The answer is that nobody could possibly do that! Any sheep-breeder or poultry-breeder who adopts what I call the nucleus system of selection starts by selecting his best males according to the quality of their (mostly female) offspring. If he does not regard the production of each female separately, nevertheless he will pick out the best group of progeny (the progeny-group of the best breeding father), and this most excellent group will be chosen as the breeding-stock for the next generation. In other words, this selection method takes the quality of the group and not the quality of the individual female as the criterion.

Why does this method of selection lead to good results? Simply because it works towards greater uniformity, and more consistent prepotency for the good qualities, or in genetic terms towards greater homozygosity, and the absence of unwanted recessives of all kinds that give us those disappointing individuals in between the good ones.

I do not blame the poultry-breeder who, even when he adopts such a system of group-selection, adds trap-nesting, in the firm belief that it can only help to make progress more rapid. If a man's customers ask for trap-nest figures he would be a poor

business man not to give them these. On the other hand, I cannot say that I think such trap-nest figures are of any considerable help in selection for production, fertility or chick mortality, unless this last is due to direct infection. I have, however, seen very many instances where a breeder was led astray by those individual records of his cows or of his hens. I have seen it happen several times that a man who was trap-nesting tended to prefer the few 300 eggers in his poorer groups to the consistently high-producing groups that gave him his best average, even when he knew quite well that those good birds from the poorer lots were sired by an inferior father. With dairy cattle, too, many intelligent farmers would prefer to raise the calves from an exceptionally productive cow of unknown pedigree rather than those from a group of 1,000 galloners that belonged to a sister group in which none produced less.

Although there are good reasons for trap-nesting and for the gathering of individual records, we must remember that such records are not in the same class with progeny-records of male breeding-stock as far as help in progress towards purity is concerned.

From the experience of breeders using the method, I contend that in poultry sufficient progress can be obtained from a method which makes no use of individual records at all, but which depends entirely upon a comparison of groups of breeding-stock produced by individual fathers within pure breeds. To conclude this chapter I will give the genetic explanation of this, for those among my readers who want to know the way a good method works.

If we choose the progeny-group that averages best from an economic standpoint, we choose the progeny of that male who happened to be homozygous for a great many important genes. Every time we continue with the descendants of a male that is homozygous for any factor in respect to which we have a proportion of heterozygotes in the group, the proportion of heterozygotes in the following generation is cut in half. For this reason the son of a proven sire must on the average be a better male himself than the general run of young males in the breed, and this relative progress, and progressive purification in the breed, will continue for as long as there are heterozygotes in respect of important genes left in the breed.

NOTES

This chapter was written apparently as one rather in the nature of an answer to criticisms and questions raised at Hagedoorn's many lectures and meetings with practical breeders. It was one of the secrets of Hagedoorn's success that even when he considered the practical breeders' arguments to be wrong—as he evidently does here—he never dismissed them as unreasonable or unworthy of careful argument and thought.

Chapter Twenty-Nine

Breeding Good Males, with the Accent on Bulls

At every sale, at every show, more money is paid for males than for females, even when the females only are directly useful, as in laying breeds of poultry or in dairy cattle. This difference in price between the sexes is really due to polygamy. This may seem surprising, as few males are necessary, and the large supply and small demand might be thought to make the males cheap. As a matter of fact the ordinary males *are* cheap, but the few that are kept as breeding-stock bring a stiff price because they have been specially selected for this purpose. In strictly monogamous animals such as pigeons and most silver foxes, breeding-stock of both sexes will bring the same price.

Good prices are paid for first-class males for breeding, when the buyer hopes that such males will produce very good offspring; and of course such good prices are justified when such hopes are reasonably well founded. Males are much more important than females statistically, as each male has so very many more descendants than any female. When we use one bull or one cock to every ten females, each male is ten times as important as a female. When, however, we employ methods that enable us to use only one cock to a hundred hens, or one bull to a thousand cows, the importance and the influence of one male is multiplied again by ten or by one hundred. There are two sides to this. It is very much more economical to use a system in which very few males suffice, but on the other hand the choosing of our males well becomes so much more difficult, as the risk of having a bad one is so great if we put too many eggs in one basket.

Of the three different methods we have of selecting our sires—

pedigree (quality of ancestors), inspection (quality of the sire as an individual), and progeny-testing (selection according to actual results)—the first two named can in some circumstances be of great value. No matter what system we employ to choose a male, however, in the end the proof of the value of those males will be obtained when the offspring show their quality.

The Value of Pedigree is Enormous. If we know from the records, that all the ancestors of a certain male belonged to a valuable breed that has been selected during very many generations, we have a guarantee that he will *on the whole* transmit the *average* hereditary make-up of his ancestors. In scientific terms, descent from a long line of pure-bred ancestors guarantees purity in respect of all the valuable *recessive* qualities of the breed, and absence of unwanted dominant qualities. It also gives us a better chance of finding the animal that will transmit valuable genes to its offspring, and that are responsible for dominant qualities, but nothing like certainty. A few very simple examples may be given. A pedigree Ayrshire bull can generally be counted upon to give horned and spotted calves, when mated to any other pedigree Ayrshire, and a Redpoll pedigree bull will almost certainly give red calves from pedigree stock. The Redpoll bull, however, may still be impure for the genes that help to make him polled or solid coloured, even if all his ancestors were solid red and polled: in fact, a good-looking pedigree Redpoll bull, bought for an experiment by an experiment station, proved to be impure in respect of both those typical Redpoll distinguishing qualities at the same time.

The Value of Personal Appearance of a ram, a cock or a bull is grossly overrated. There are two things that make appearance valuable, and the more important of these is that a non-registered animal of unknown origin that shows all the earmarks of some breed is more likely to be a pure-bred than a cross-bred. For this reason open herd-books that register grades insist on inspection. Within the breed the system of showing and of breeding for shows makes it exceedingly profitable for the lucky owner of some beast that the judge likes the look of, to sell his champion or its offspring. The gamble of breeding show stock is very exciting, and much money is spent on it by many, and won by a few. In itself, however, it is of no intrinsic direct value

to agriculture. Breeders and fanciers always strive to justify this game in their own eyes (or in those of their wives) by making each other believe that it is possible to pick out the most useful animals by simple inspection. There is no proof of this, but the fancy—except for its attendant hypocrisies—does no harm as long as it does not interfere with serious animal breeding (as it may sometimes do when bulls or stallions have to be licensed, by officials trained at the shows).

The Value of Progeny-testing lies in the fact that it does not depend upon any theory but upon *actual results*. When we want a profitable barley or potato we try out a few kinds and choose the one that suits our soil or our climate, rather than depend upon what the seedsmen say in their catalogues. If we want a breed of poultry or an individual cock, a breed of sheep or a single ram, the safest way is to try out a few and pick the best one. When such testing out becomes expensive or risky, we can often delegate this work to the local agricultural authorities. The agricultural experiment stations have been doing this work for farmers for a long time as far as crops are concerned, and the Milk Marketing Board has recently started doing it in respect of dairy cattle in England.

Where do we obtain Good Males? When we need some bulls for a number of A.I. centres, some cocks for a hatchery that wants to give its customers good chicks, or some rams to head our flocks, we must do all we can to obtain the very best ones for our purpose. We can either find them and buy them, or we can breed them ourselves.

Whether it is better and cheaper to obtain bulls and cocks and rams from the other breeders, or to breed them ourselves, depends upon a great many things but especially on the *rate of increase*. When the rate of increase is very great, as in cattle under A.I., and when the males, once found, will remain in service for a long time, it will often be cheapest to buy them. Where are we going to find them?

Producing males for breeding purposes is a specialist's job. It is a highly-specialized job that should pay very good profits.

In the vast majority of instances the males we need are pedigree stock—and the pedigree breeders have done excellent work with the means at their disposal. They have kept the breeds

separate, and by their system of individual selection, they have brought them to a state of relative purity. In most of the breeds of cattle, sheep and poultry, the best outstanding individuals are excellent. That is to say, some of the stock, the majority, come up to the fancy standard of beauty, and a few of these in every generation are show champions, while the majority of animals in the breed are very good from an economic standpoint, with a few superlatively good individuals amongst them. As a rule, within each breed, variation from a standpoint of the fancy and variation from the standpoint of utility are independent, so that too much emphasis on show-points just makes it more difficult to find economically useful stock.

Why do we find all this variation even in pure-bred stock? Why so many that are just ordinary, why so many culls? Part of this variation is certainly due to adverse circumstances, to infection in youth, to mineral, chemical and vitamin deficiencies, or conversely, to feeding plenty of full milk to the prizewinners. Part of it, however, is certainly genetic. To state it in terms of genetics, even excellent stock may give some wasters when some of the breeding-stock is heterozygous for the genes we need in our potentially excellent young stock. To put it briefly, if not entirely accurately (for even dominance may be reversed in hopelessly impure stock), pedigree pure-bred stock is pure in respect to recessive and partially dominant qualities, but often very, very impure in regard to many desirable dominants.

What are we looking for when progeny-testing males? If we are dealing with pure-bred stock and not with mongrels, we are looking for males that are sure to transmit the desirable genes to all their offspring, so that they will have no descendants that are handicapped by inherited deficiencies. One thing is certain, most pedigree breeds I know are very far from pure in this respect. This can be shown by the fact that in-breeding in almost any breed will produce some genetically inferior young stock.

A very good, prepotent male will very often sire daughters that are better than their mothers. This is especially so when we are mating him to very heterogenous and cross-bred female stock: yet, within a "pure" breed this ability of a male to raise the quality of his daughters above that of their dams is not a safe criterion for very long use, except in grading herds. For several

reasons, both scientific and practical, I prefer the very simplest test of all, the examination of a representative sample of a male's progeny. As I said in my first book on animal breeding (1912): "The only correct way to judge a bull (in respect of butter-fat production) is to test all his daughters."

The Preferent Bull Scheme in Holland and Friesland, which tests a bull's ability to give good-looking as well as useful offspring, and the British Register of Merit Scheme, which looks for productive daughters, are incomplete insofar as they leave eventual culls out of consideration, but within the work of the breed societies those schemes had the useful tendency of drawing some official attention to production as well as to show-points. The Danish and several American schemes, which take the production of aberrant and disappointing offspring into account, are decidedly preferable.

Breeding from excellent and beautiful cows only, however, as in the older schemes, has had at least this good point, that even if the breeds are variable, they still contain a proportion of profitable and good-looking stock, so that pedigree cattle—and the same is true for pigs, poultry and sheep—give us excellent foundation-stock to work with.

The pessimists in the councils of cattle breed societies used to condemn any system of looking for proven bulls, by telling us that no bulls exist that will never give an aberrant or a worthless calf, and that it would be a waste of money to raise any really inferior heifers to test the sire. It is certainly true, however, that in several progeny-testing schemes there have been found bulls whose daughters are all profitable. We must also realize that homozygosity in this respect is only comparative and relative.

In cattle, sheep, pigs and poultry, we know a good many more or less rare defects that are certainly due to genetical deficiencies, and it is important that we should recognize them as soon as they occur. It is certain that such defects may originate "spontaneously", although my own experiments show that such quasi-mutations are often due to breed-crosses. If dominant aberrations are selected against, they disappear. In all cases of inferiority that are difficult to eradicate we are dealing with recessives, and just breeding the best to the best will not help us to get rid of the trouble.

Recessive defects range from fatal things that cause death of the embryo, foetal atrophy, dying germs, dead-in-shell,

malformations, amputations, dwarfness, blindness, deafness, inability to stand, to more subtle ones that cause high susceptibility to disease, trouble with feathering in chicks, aberrant instinct down to plain stupidity, and unanalysable instances of "doing badly". Economically the worst cases are those in which the inferiority is not noticed until the animal has been raised to maturity, as in barrenness in heifers, progressive blindness in hunting-dogs, mental defects in racehorses, paralysis in fowls.

Although in a few instances it would be possible deliberately to test a great many animals for homozygosis in respect to any of those genes, and to form a group that would consist of homozygotes only, I very seldom counsel breeders to follow such a plan. It is very much wiser to restrict our attention and efforts to the *males*, and here a general system of progeny-testing will serve very much better and more safely than test-matings.

The explanation is simple enough. Let us suppose we are dealing with some gene, *A*, which has such an effect on growth and development that the *AA* and the *Aa* individuals are good, whereas the *aa*'s are defective. The group consists of a great majority of *AA*'s with an occasional *Aa* mixed in. Every time two *Aa*'s happen to be mated together, there is one chance in four that an aberrant individual is born. (From the beginning we must keep in the back of our minds that in the same material exactly the same may be true in respect to genes *B* and *C* and *D* and thirty others.)

A male is mated to ten or to a hundred females. If that male is an *AA* one, he can never have an *aa* son or daughter, no matter if some of his mates were heterozygous, *Aa*. If, however, our male is heterozygous, *Aa*, there is a 25 per cent. chance of the birth of an aberrant young from any mating of our male to *Aa* females. If a great many cases of the aberration have been met with in the breed or strain we want to ameliorate, mating that male to a dozen females might show him up as a heterozygote (*Aa*). The rarer the aberration is, in other words, the lower the proportion of *Aa*'s in the group of mainly *AA* ones, the more females our male must be mated with to make sure that he *is* "carrying the defect". The number of matings necessary to "prove" a bull or a ram, a dog or a cock, will depend upon the proportion of heterozygous females in that group, and the number of young born from each mating. We can greatly ameliorate the method by doing what Wriedt proposed, test-

mating a male to a group of his own daughters. If we do this, an *Aa* male will always have 50 per cent. of similar (*Aa*) daughters, so that there is one chance in every eight that his offspring will be defective (*aa*). Mating a cock with four to six daughters (several chicks from each mate) will be enough, and mating a dog to six of his own daughters ought to be enough, but in the case of a ram or a stallion or a bull we ought to have at least a dozen daughters, because here a mating does not give a litter.

If for any reason we do not want to wait for all this, we may speed up the process by taking sisters, to test-mate a male. Here we start from the knowledge that a heterozygous male (*Aa*) must have had at least one heterozygous parent, so half his full sisters must also be heterozygous.

When we are dealing with very serious defects, such as blindness or deafness in hunting-dogs, or bad fertility in cattle or fowls, deliberate test-matings of males to their own sisters or daughters is certainly indicated. A special certificate for breeding-males that would be shown to have given no definitely aberrant offspring and excellent fertility from a stated number of their own daughters, would be of exceedingly great value, in relation to rams, bulls, stallions or stud dogs. Wriedt has proposed the establishment of such certificates for farm livestock, and I have recently proposed doing the same thing for dogs where it would be a god-send to gun-dog breeders looking for safe sires.

In all I have said so far I have taken it for granted that in all this progeny-testing we were working on the males. Why the males? In the first place because in any polygamous group the males are several times as important as the females, and in the second place because it is almost hopelessly impossible to progeny-test females.

Will progeny-testing the males alone help towards purity? To answer this question we must remember that a male that has been definitely proved to be homozygous in respect to any gene will have no offspring lacking it (this is implied in the definition). A bull, chosen for work in an A.I. centre after he has been shown to give nothing but typical healthy and productive daughters in a large enough unselected sample from cows of his own breed and family, can be counted upon to give many thousands of good daughters if his sperm is diluted far enough. The

use of a succession of closely-related proven sires in a closed nucleus will double the proportion of homozygotes per generation in respect to any of the genes involved, even if the females are never progeny-tested.

To answer the question if we could speed up this process by progeny-testing the females as well as the males, it will help if we see how much we could get to know about a male by mating him to just one female. We start with the assumption that we are dealing with an instance of complete dominance, so that *AA* animals are not distinguishable from *Aa* ones by any direct inspection. To test one male by mating him to one female, we would have to know for certain that this female was heterozygous (*Aa*), let us say a cow (or ewe or hen) that had already given some aberrant, off-coloured or defective young. In such an event we might feel safe when from this one female we had six or eight perfect offspring. On the other hand, proving a bull by examining his offspring from just one *good* breeding cow (even if she gave us a dozen calves) would be very unsatisfactory.

Exactly the same is true when progeny-testing the females. One individual cow or hen or bitch that has given us several perfectly good and valuable descendants can never be said to be a good breeder in the sense of the progeny-test for purity, unless that group of offspring were from at least four to six males preferably very closely related to her. In trap-nesting hens or ducks, we repeatedly find that one female that has given half a dozen excellent daughters from very fertile eggs, when mated to one male, will when mated to another male give several chicks dead in shell, or a few very disappointing daughters. It is very profitable for a dairyman to own an excellent cow that has given two or three very fine daughters with high yield, but to think that this old cow for that reason is the ideal mother of bulls would be much too optimistic.

What we want in our breeding-stock is prepotency or purity, and in genetic terms prepotency means being homozygous for all the important genetic factors known or unknown. A prepotent ram is a ram that will give the right set of genes to all his get; a prepotent bull is one whose offspring are profitable without exception. If we need such males for an A.I. scheme we must go to the pedigree breeders to find them. Why? Are not the pedigree bulls very often impure for the very things we want

most? Of course they are, as every breeder knows from bitter experience, but the very fact that such pedigree families are closely bred (relatively in-bred) makes the potential variability of this stock relatively low—necessarily lower than the good-looking low grades and their good-looking sons. Pedigree stock, however, must be considered as foundation-stock that now has to be consolidated and ameliorated by further in-breeding and by more efficient methods of selection for the very thing practical breeders want—purity and prepotency.

I am firmly convinced the pedigree breeders will have to do this for the good of agriculture, and it will be to their very great interest to do this work. So far the breeding of pedigree stock has been too much bound up with the cattle show game. Breeding show animals is still profitable, so long as foreign buyers can be attracted—but farming everywhere is getting more and more efficient, and if overseas customers want profitable pure-breeding dairy cattle they are more and more likely to buy them where very reliable breeding-stock is being produced as a result of rational systems of selection, even if the professional foreign cattle-showmen will be coming for a few head now and then, for the show circuits.

Breeding excellent bulls for the A.I. centres and for private breeders is certainly likely to bring more satisfaction to serious-minded breeders than just trying to breed something that will please the judge at a show! Is it difficult?

Perhaps it is a consolation if I say that whereas breeding for the fancy means striving towards an ever-receding goal that is shifting with the fashion of the day, breeding for utility is breeding towards a fixed set of aims, profit resulting from the difference between outgoings (rent, labour and food) and incoming (milk cheques, stores and breeding-stock). Breeding for the shows will always remain difficult; breeding for profit will become less and less difficult when reasonable purity is being attained.

Since Odlum wrote his *Manningford Analysis*, the greatest book on breeding profitable cattle I have ever seen, pedigree breeders have an ideal guide how to do the work, and a perfect answer to all the questions that are bound to crop up. The book also shows the enormous danger of leaving to the hazards of chance the efforts of an excellent breeder to establish a nucleus herd for the good of the farming community. The breed societies should

foster the establishment of similar nuclei, safe from the ravages of professional jealousy. I am hardly optimistic enough to dare hope that the breed society councils will take up this task before the middle of next century. If the private breeders will not grasp this opportunity, I am very certain the Milk Marketing Board will be able to do it very well indeed, establishing nucleus herds of pedigree cattle for the in-breeding and genotypic selection necessary to produce good bulls, testing them in connexion with the A.I. work, and keeping them in cold storage until the few outstanding prepotent ones will be discovered and used with thousands of cows. What a chance, however, for an intelligent private breeder with the necessary capital!

NOTES

In discussing the various criteria for selection of males with particular reference to dairy bulls, Hagedoorn discusses three in turn:

(a) *Pedigree*

(b) *Phenotype*

(c) *Progeny.*

Quite rightly he gives greatest weight to (c). *In stating however that "The value of pedigree is enormous", I feel myself that he is going beyond the facts and in a sense contradicting a great deal of his own teaching. If the value of pedigree were "enormous" there would be less need for progeny-testing, and it is indeed on the proven inadequacy of "pedigree" as a basis for selection that the necessity for progeny-testing has arisen.*

Chapter Thirty

Breeding the Horns Off

Since the end of the second world war, cattle-breeders all over the world have seemed to be anxious to "breed the horns off" some of the most diverse breeds.

In England I have been discussing the possibilities of dehorning cattle with owners of three different breeds, and in two places the necessary work has been well started.

Breeding the horns off cattle in breeds that have always carried them is a good example of a straightforward and relatively simple genetic problem, and it illustrates the difference between one of the very simplest genetic "recipes" and the actual complex process of carrying out the work in practice.

Let me start by giving the instructions such as I give them to the breeders who want to establish a polled sub-variety of some useful breed of cattle. As polledness is dominant, all the breeder needs to do is to cross his breed with some polled animals, take the polled hybrids and breed them back repeatedly with very good animals of the breed for five or six generations, until he has succeeded in getting his original breed back in all its purity, but minus the horns. After this he will have to produce some homozygous polled animals by inter-crossing, and selection of the pure-breeding ones among the offspring of the inter-bred generation.

This is all very simple on paper. Adding one gene to an existing breed is just what I did in making my first autosexing Barnevelders (see p. 52). Now for the difficulties. The first difficulties are technical, and the first question to be answered is which of the polled breeds shall be used for the work. There are two sides to this question. In some breeds, such as the Hereford and the Ayrshire, polled sub-sections of the breed already exist.

It would be quite feasible for an English breeder of either Hereford or Ayrshire to obtain some sperm from a pure-bred registered polled sire, have it flown over from the U.S.A. and produce some polled pure-bred calves. This would save the breeder at least five generations, a matter of ten to fifteen years!

If for some reason this seems out of the question, so that the breeder will have to go the long way of repeated back-crosses, it is not impossible that careful inquiries will find some non-pedigree polled animals in the breed to be dehorned. In the autumn of 1946 I was shown a few polled Dairy Shorthorn cows that had every appearance of better-quality ordinary examples of the breed. By starting with such animals as one may find, two or three or even more generations of breeding work can easily be saved. For several reasons it would be a great saving of time and money if one could find pure-bred, pedigree "freaks"—pedigree pure-bred animals born without horns. Mr. Victor Berger of Stoke Hammond has located a few head of pure-bred Guernseys that are naturally polled, and he is on the look-out for a few more of them. The Americans tell us that the first polled Herefords were freaks found in pedigree herds, and although on the face of it such a "mutation" seems very improbable, I would not be too emphatic about it. So much is certain, that the pure-bred Herefords of the polled sub-sections both in America and in the Argentine are seldom up to the show standard of the horned sub-section, or seldom as good as the polled animals with one horned parent. This would indicate that even in this instance the polled beasts originated from a (remote) cross.

If for some reason no polled individuals of the breed are available, so that a cross is indicated, I should judge that it does not matter very much which polled breed is employed.

At one of the agricultural experiment stations a Redpoll bull has been bought to dehorn the Ayrshires. If such a bull employed is pure-bred, he should give nothing but polled calves, even when their mothers are horned. The particular Redpoll bull happened to be heterozygous in respect to two of the factors concerned, for only half of his offspring were polled, and some of his calves were spotted. In this particular case any chance polled bull bought at the market would have done as well as this pedigree bull.

Is it necessary to use a pedigree, pure-bred bull of a polled

breed for this purpose? I should think there is not the slightest advantage in getting an expensive bull, for the cross-breeding will destroy any homozygosity in any case.

The first cross-breds should be mated back to the breed to be dehorned, and only the polled calves (50 per cent.) should be saved for use. It is evident that this takes a very long time, for at least five back-crosses should be made, before the graded animals should be mated *inter se* to produce the homozygous, pure-breeding polled Ayrshires (or Lincoln Reds, or Herefords, etc.).

I know from experience that every breeder who engages in such a scheme wants to discuss cutting down the time required for the process—and it will be possible to save time in different ways. In the first place, it will be possible to do the cross-breeding and back-crossing in the male line, using the polled males as soon as they are ready for breeding. This saves time, but it makes selection for yield or conformation impossible. This, indeed, is not very serious, as selection during a repeated series of back-crosses should be unnecessary, for we must rely upon the average excellent quality of the family or families in the breed we want to dehorn.

A much more serious objection to the use of male cross-breds for grading up lies in regulations existing in some countries that require the licensing of breeding bulls. Such measures (of very doubtful value anyhow) might interfere with the work, and might force the breeder or the experiment station to proceed in the female line just to obviate interference by well-meaning and zealous officials, who might not be too well grounded in genetics.

A more obvious way to save time is using imported sperm from pedigree bulls of an American polled section of the herd-book such as we know exist in Ayrshire, Hereford, Friesian and Guernsey, in the U.S.A. I have already spoken of the occasional polled "freak" that can be found in the market, and that is probably simply a graded beast derived from some forgotten cross of a few generations ago.

Since this book first appeared in England a great many breeders have started dehorning different old breeds to take advantage of the greater docility and absence of bullying resulting from the absence of horns. In discussions in the weekly press it has been often proposed to cut down the number of generations

required, by inter-breeding the first or second generation of good-looking cross-breds. It is, indeed, a great temptation to a breeder who has, by one back-cross, produced some excellent and typical heifers, to breed those beasts to a similar cross-bred and good-looking bull. It has been urged that in theory one could produce pure-breeding and excellent breeding-stock in this way, provided we took the numbers large enough to find the necessary homozygotes in respect of half a dozen important genes. This is certainly true—on paper!—but I must emphatically warn everybody against this. If we knew that we were only concerned with half a dozen genes, we could easily calculate the number of second-generation animals necessary to produce a proven bull, homozygous for all those genes. In such an event we would only have to test about a thousand second-generation bulls, by suitable test-matings: but what about the possibility, nay, the probability, that we are really dealing with twenty or thirty important genes?

Even in poultry, where fertility is so much greater, and maturity comes so much earlier, inter-breeding of hybrids in order to produce novel breeds is very, very risky. An actual example is given by the difference between the Legbar, which was produced by selection from cross-bred fowls, and the auto-sexing Leghorn, which was made by bringing the sex chromosome from Cuckoo Leghorn into a highly in-bred strain of Brown Leghorn by repeated back-crosses. The difference in purity, egg colour and production in this instance is wholly due to the fact that advantage was taken of those qualities in this one particular strain of Brown Leghorns, breeding back to this strain repeatedly even if it took a few more years to get the final results.

The advantage of repeated back-crosses over breeding hybrids together is not only that this back-crossing automatically makes for greater purity, but it also makes it possible to do the work with half a dozen animals per generation instead of with several thousand!

Inevitably in every scheme of this kind the question comes up, whether it will or will not be possible to retain some point of superiority possessed by some of the cross-bred animals as compared with their pure-bred relatives. I always tell my correspondents that just plain routine back-crossing will give them their own pure breed back as it is to-day with that one single gene added. Perhaps it is necessary at this point to assure my

geneticist friends that I am very well aware that we can only be sure of substituting an entire chromosome, not just one gene, although crossing over should dispose of most of the other genes on that chromosome in several back-crosses.

A more complete answer to the question depends upon two things—upon the actual outcome of the first back-crosses, and upon the possibility of keeping twenty to thirty beasts in every generation instead of half a dozen. If this is not excluded—and in breeding stations it should be possible—then a second dominant characteristic in addition to just absence of horns could be kept in and retained in the final herd.

In the literature on polling cattle some authors are very emphatic in their statement that the heterozygous animals bear scurs. My experience was that they are completely polled. For this reason I was very much interested in the first results of some of my correspondents. Obviously it would be an enormous advantage if we could in the end recognize homozygous from heterozygous polled cattle. If the statement were true, it would be extremely simple to tell the homozygous polled animals from the impure ones as soon as we obtained an inter-bred generation after grading up. In none of the cases I have been able to follow up, however, was it true, notwithstanding the fact that some of my colleagues in their diagrams have assumed the heterozygotes to carry scurs. It may be true in some instances, but in Hereford, in Aberdeen-Angus × Lincoln Red and in Redpolls no difference between homozygotes and heterozygotes is discernible.

Most of the polling projects with cattle are of comparatively recent origin, and for this reason it is very interesting to be able to quote one recent advanced instance. Mr. C. Munnings of Heathcote, New Zealand, tells me that he has bought a Coates Herd-book polled bull by a son of an American polled cow out of the same cow's polled granddaughter. He has been mated to twelve Coates Herd-book cows, as my correspondent has to work through this book in order to enter the stock in the New Zealand Milking Shorthorn Herd-book eventually. Soon this breeder will have something absolutely unique, a pedigree polled Coates Herd-book stud! Some of the very best proven bulls in New Zealand have gone into the making of this.

Many examples from overseas have helped to convince the authorities that it would pay the pedigree breeders in England

to keep abreast of the times if their foreign and colonial customers are resolved to do away with the horns. The export trade in cattle is not as important as it used to be, but I suppose it is worth while saving it if it can be done.

Mr. Eric L. C. Pentecost of Nottinghamshire was the first British breeder in modern times to deliberately dehorn a well-known breed by genetic means, i.e. by the adding of a gene (or substituting a chromosome carrying it) from another breed.

After some correspondence he used Red Aberdeen-Angus males and then back-crossed the polled females for four or five generations to males of Lincoln Red Shorthorn, continuing always from the polled ones. He has now come to the stage where the heifer calves will be used for interbreeding and he has agreed with the Lincoln Red Shorthorn Society to pass the benefits of his work to them by registering these heifers as foundation females of the new polled breed (or section). With regard to bulls, only polled bulls which are homozygous for the polled gene may be registered with the Society; for it is Mr. Pentecost's object, with which the Lincoln Red Shorthorn Society concur, to make the separate polled section so that all animals registered will breed 100 per cent. true to polling, like the Aberdeen-Angus or Galloway, by the use right from the beginning of homozygous polled bulls.

Occasionally a hornless ram appears in a merino flock. In 934 T. S. Falkiner & Sons of New South Wales started to breed a polled merino stud (Fig. 37). The interest in polled rams is due to the following considerations. The natural horns are entirely without practical use, but they have disadvantages: (1) The rams with horns have to carry on their head considerable weight, a great disadvantage in hard times when they have to walk long distances. (2) Flies strike at the base of the horn on account of a special odour: this is probably the most serious menace. (3) Rams with horns are caught in fences and die, or two become locked together and both die. (4) Hornless rams are usually in the lead, heads well up in walking, indicating the advantage they have without these obstructions. (5) Station people from the outback report that hornless rams do better, live longer, are more active and more likely to escape their enemies. Mr E. H. (later Sir Edward) Lefroy, himself a breeder of polled merinos, who sent these details, thinks that in the long run the merino will be predominantly a polled breed.

NOTES

There is little to add to this chapter which contains all the advice offered by the geneticist to the numerous Breed Societies now engaged in the business of establishing polled varieties of horned breeds. In justice to the practical breeder it should be added that he succeeded in establishing polled breeds before there were any geneticists available to advise him. Both Aberdeen-Angus and Galloway cattle are descended from ancestors of which many were horned.

Chapter Thirty-One

Pedigree

When we thought inheritance was the transmittance of an ancestor's qualities to his descendants it seemed very important to know the qualities of the ancestors of an animal, because we thought this quality of the ancestry gave the animal not only its own characters but also the power to transmit good quality.

The result has been that, wherever breeders and fanciers were interested in pure breeds, pedigrees have been kept up religiously. Some breeders still think that it makes an animal more valuable when it can be proved that among its ancestors the names of famous well-known animals occur.

With a better understanding of heredity, due to a development of the science of Genetics, much of this value of pedigree disappears. We now know that it is not the qualities of an animal that are inherited, but one special kind of substance in the cell-nucleus, which when co-operating with favourable environmental factors give an animal its qualities. Heredity is the transmittance of these genes. Even, however, as far as we could think of those genes as "determinants" for certain characters, it cannot be said that an animal which shows the possession of a certain gene must necessarily pass this gene on to its children. An animal, excellent in itself, may be heterozygous for important genes, and an animal heterozygous for a gene only passes it on to one-half of its children.

In certain cases a good pedigree may be of value, namely, where it can be learned from it that all ancestors have belonged to one breed, so that cross-breeding has not taken place recently. On the other hand, it is unnecessary to know anything about the more distant ancestors, when the make-up of the parents

is sufficiently known. In our mouse colony we have a few highly-in-bred, entirely homozygous strains. It is sufficient to know that a certain mouse is born from two parents of the Little cancer strain, to know exactly what its constitution is, how it will react under given circumstances and so on. In such instances as in that of the black Lahore pigeon, the Wistar Institute albino rat, and a few similar pure strains, knowledge about ancestors is entirely superfluous, it suffices to know that both parents belonged to the pure strain.

Often, a study of an animal's pedigree will give us an entirely wrong idea about its qualities. In herd-books where selective registration is the rule, a pedigree will only contain the names of animals approved by the registration committee; but this pedigree teaches us very little about the probable qualities of a young animal. It seems plausible to believe that long lines of only superior ancestors give a good guarantee of quality; but this is entirely erroneous.

An example will illustrate this. In the Blue Andalusian fowl all blue animals are heterozygous. Mating blue with blue gives only 50 per cent. blues. When we study the pedigree of a Blue Andalusian cock, its parents, grandparents, great-grandparents and so on are all seen to have been blue. We know that they have all been heterozygous, but this does not appear from the pedigree, and we know the pedigreed cock to be heterozygous, although this cannot be inferred from the pedigree.

The good qualities which make the ancestors of an animal eligible for registration, may be very largely due to environmental circumstances. In circumstances like that of the Dutch marked rabbit, the registered ancestors of a young animal are all perfectly marked. They do not, however, differ genetically from the non-registered mismarked relatives, and the fact that all ancestors were perfectly marked, does not make it more probable that the young animal will have good markings, or will breed young stock with good markings.

In earlier years the craze for beautiful pedigrees assumed much greater proportions than nowadays. I remember in my Californian days a heated controversy between Jack London and Mr. Hillier, two owners of Jersey bulls, who both claimed to own the "best-bred bull" in California! The dispute was formally settled by a committee examining both pedigrees. The actual quality of the bulls as breeders did not get discussed at all.

The necessity of furnishing accurate and imposing pedigrees with all livestock sold was the first object in the establishment of herd-books. For this reason the administration of the register is generally so arranged that in any given case it is possible to find the ancestors of an animal at a glance, whereas it is practically impossible to work in the other direction, and to look up the descendants of a given animal. I am proud to say that, as already indicated, the two cattle herd-books in Holland now have a card index, which makes it possible to find which animals are the children of a given bull.

Now that a few cattle herd-books have realized the importance of bull testing and regularly publish the average yield of a bull's daughters, they will be forced to give more attention to genotype and performance than to mere pedigree.

The pedigree of an animal, when sufficient data are given about the ancestors, including the results of progeny-testing, would be a very valuable guide to help guess its breeding value. It is clear that, when we know that an animal descends from a long line of prepotent (homozygous) sires, the chance that it may turn out a good one looks brighter. One or two famous males in the ancestry, even such data as the proof of descent from a "preferent" bull, are of very little value as a guide in buying livestock.

As a rule the prices paid for pedigree stock are much too high in relation to the probability of quality. This is profitable for the herd-book members, who are out to make profit from the sale of breeding stock, but it often leads to disappointment, and therefore tends to make the breeding of such stock risky.

The faith in a beautiful pedigree is often astonishing. I remember how the Dutch agricultural press wrote about the "breeding value" of a bull sold to a Japanese delegation, in terms that made one think this must have been a bull proven by long lists of exceptionally good daughters. It was said to be a pity that such bulls were sold to foreigners. When the article went on to state that the bull was ten months old, one wondered about the faith Orientals still seem to have in ancestry.

As long as customers of livestock set great value upon pedigree, it will pay to sell calves and foals and piglets with official papers: but I do believe it is high time that the intelligent breeders themselves should know that the value of such papers is greatly overrated.

When pedigrees are issued with breeding stock it is important that the pedigree shall be correct: not so much from a genetic standpoint, for so long as the parents and grandparents are truly named, the rest is of small importance, as the chance that an animal derives one of its chromosomes from a far-removed ancestor is very small indeed. The customer, who believes in pedigree, wants to be sure that the pedigree is correct. This has been one of the reasons for the State Herd-books in Canada. Some herd-books are much more honest and strict than others, but the general trend is toward honesty in these things. The time when it was possible to buy official papers with a foal bought in the market, and when it was found that one mare had four sons credited to it as born within one year, is past.

I believe that in the matter of pedigrees the time will soon come when breeders will clamour for reorganization in herd-book methods, and that the days when a bare pedigree that only gave the names of all the ancestors was considered of great value are past.

NOTES

At the end of this chapter Hagedoorn wrote: ". . . that the days when a bare pedigree that only gave the names of all the ancestors was considered of great value are past." I would suggest the substitution of the word "passing" for "past". I feel that the word "pedigree" when applied to livestock is still generally accepted as being synonymous with superiority. The statement that pedigree is merely a record of ancestry, sometimes of doubtless authenticity, is still regarded as being somewhat heretical.

Chapter Thirty-Two

The Nucleus Scheme of Pedigree Breeding

In all of the important domestic animals and birds, the object of selection is to improve the average quality of the stock. The users want groups of animals that are very much alike because, for obvious reasons, great similarity is worth so much that the presence of occasional superlatively good individuals in a mixed lot does not compensate for great variability.

The farmer's ideal is a group in which no aberrant, comparatively worthless young individuals are born; he wants cattle or sheep or poultry that react in the same way to the same treatment—animals that start producing at the same time and that during production can be treated alike.

Mass selection, the ordinary system of selection in livestock, generally tends to produce flocks and herds of domestic animals in which harmful dominants have been bred out, but in which many animals are heterozygous for desirable genes, so that unwanted recessives often crop up in every generation. On the whole, the chief problem before all breeders of farm livestock is the purification of their best groups of animals. If the farmer can have livestock that are as good on the average as the best of his present animals, barring the very few superlative show individuals, he is satisfied. This means that we must try to work in such a way that this goal is reached.

Mass selection will never do it, for wherever the animals that are heterozygous for an important factor are indistinguishable from the homozygotes, these heterozygotes will keep on breeding and reproducing the unwanted recessives. A system of selection that consists of weeding out the recessives and which leaves the heterozygotes is very ineffective.

In the chapter on test-mating I showed that, wherever it is

possible to ensure that all the males procreating in any one generation are homozygous for a given gene, the proportion of heterozygotes in the next generation is halved. This is true of every gene for which the breed is not yet pure.

Now it stands to reason that it is impossible to employ deliberate test-matings to find males homozygous for all the important genes in a large population of animals or birds such as one of the popular breeds. In the first place we do not know those genes as such, or only a few of them; and in the second place this would necessitate an enormous amount of experimental work.

Wherever we do not know the gene, or the combination of genes, that must be present in our best animals, we can substitute progeny-tests for test-matings. When a certain proportion of animals in a population is impure (heterozygous) in regard to the many genes we want to see in all our animals, a male will be mated to several heterozygous females. If, for this reason, we know the quality of a great number of his descendants, we get a clear picture of his homozygosity in respect of quite a number of genes.

It is evident, however, that even test-mating is not a method that can be applied to all breeding males without turning the present system of breeding animals upside down. Most males are of very little importance in the breed, and it would be a waste of energy to work in such a way that even those males would have to be tested.

It is possible to propose a system of selection that makes the fullest use of progeny-testing to get the result we want—great purity of the breed in respect of all the most valuable qualities.

To do this we must realize how a breed of animals is generally propagated. Roughly, we can distinguish in any breed of animals a relatively small group of animals or birds of high quality in the hands of a few pedigree breeders, while the majority of the breed is in the hands of the common farmers who use the animals for commercial purposes. This larger group of farmers, the users of the breed, tend to look up to the pedigree breeders, and the pedigree breeders sell breeding stock, mainly male breeding stock, to the farmers with the object of improving the quality of the farmers' animals.

This system is excellent in principle. If we examine it in detail, however, we immediately see the very obvious flaws, and

it must be our object to retain the good qualities of the present system and to make it more efficient than it is.

As all our most important domestic animals, the horse, cattle, swine, sheep, poultry, are polygamous, a very few males suffice in each breed, and as half of the young born are males, it is evident that a relatively small nucleus of excellent breeding stock is sufficient to produce all the males needed in the whole breed.

When, however, we investigate the quality of the animals in the hands of the pedigree breeders and compare this quality with that of the common herds, we see that very often the difference is too small. Often the difference lies mainly in superficial things, in show points, in markings, in the set of the tail, in eye colour, and it is evident that the system of agricultural shows is mainly destined to establish an artificial standard of value, that confers on the animals in the hands of the pedigree breeders an artificial superiority that is in no obvious way related to real economic superiority.

Worse still, when we really delve down to facts we find that the beautiful pedigree animals, the champions of our shows, are in no way pure for the very inherited factors that help to make them beautiful. It was an unpleasant surprise to many herd-book members when recent researches on the inheritance of show points in cattle indicated that, if one is especially anxious to breed heifers with all those marks of superiority, with straight backs, heavy legs, well-set-on tails, one is as likely to produce them from a cheap bull that has no very great claim to beauty in regard to those points as from a show champion that exhibits all those admired qualities to perfection. The pedigree stock can certainly not claim superiority because of great homozygosity, not even in so far as concerns genes that help to produce the wanted show points.

As regards economic quality, wherever an unbiased investigation is made into the relative merit of pedigree and non-pedigree animals—horses, swine or cattle—the result is always the same; if a difference exists, it is always slight, and generally the non-pedigree animals are just slightly more valuable economically.

I am certainly no great admirer of the results of pedigree breeding in farm animals and yet I maintain that even if the claims of the pedigree breeders were wholly unfounded, the system, which is based upon the idea that pedigree stock is more

valuable, should be retained. It is high time, however, that we geneticists should help to produce a state of things where pedigree stock really is more valuable than non-selected stock!

The reason why I want to retain the system of breeding that consists of maintaining a nucleus of excellent stock in every breed from which males are produced for the rest of the breed, is as follows.

When our aim is purity for that set of genes that we now have in our very good animals, we must work in such a way that the variability in the breed is lowered. As already observed earlier, I once introduced the term "total potential variability" for the number of genes in regard to which a group of animals is not pure. The total potential variability tends to be raised by cross-breeding, and very rare mutations, and to reduce itself automatically in every group that is closed to admixture of outside individuals.

The reduction of variability of a group is much more rapid in small groups than in big ones. It is rather a complicated business to calculate this reduction of the variability, but Lush has given simplified formulæ to make a sufficiently accurate calculation for our present purpose. We can calculate the proportion of the potential variability that is lost in one generation. If we call F the number of females in the group and M the number of males, the proportion of the potential variability lost in one generation is about $\frac{1}{8F} + \frac{1}{8M}$. In polygamous animals where the number of females to every male is very large, F is very large in proportion to M, and for this reason the number of males in the group really determines the proportion of the potential variability that is lost in one generation (in-breeding rate). The formula then becomes $1/8M$. In a group in which 10 males are used, $1/80$ is lost, in a group with 100 males only $1/800$ is lost, but in a group with only one sire, $1/8$ of the potential variability is lost in one generation.

This means that in a breed where several hundred males are used in every generation, there is really no purification worth talking about. It is not probable that in the breeds in which great numbers of animals are bred in every generation, selection can have done very much to change the breed. The obvious changes we meet in such breeds are really due to the fact that what we consider as one breed really consists of several relatively

unrelated families of different quality. In such circumstances one family in which the animals are better adapted to special conditions will gradually supplant all the other families, generally by a system of "grading". It would therefore be almost a hopeless task to improve a numerous breed of animals by mass selection.

When, however, we utilize the system of having a central nucleus to produce males for the whole breed, everything changes; for in such a nucleus we can reduce the number of males, and in doing this we make the proportion of the remaining variability considerably smaller.

When M, the number of males in the group, becomes small, $1/8M$ becomes relatively larger. The ideal in the nucleus herd must be to use as few males as possible. This is important in two different ways. The fewer males we use in the nucleus herd, the stricter can be our selection, and the greater slice of impurity is done away with per generation (see Fig. 22).

Let us suppose we could draw up a strict set of regulations to control the breeding of some breed of animals in a country. The best way to do this would be to establish a nucleus group that would be so bred that in this group the quality would rapidly improve and the impurities would rapidly diminish. The next step would be to make it obligatory to use only males produced from the nucleus group in the propagation of the breed.

The best way to discuss such regulations is to use an actual example. The breeding of swine in Holland and Germany is effectively regulated by the Government, and every piglet born is tattooed and numbered.

In the first place we must know how large our nucleus herd must be. Let us take actual figures from Holland. In Holland there are 150,000 breeding sows and 5,000 breeding boars. This means that every boar produces on the average 30 litters twice a year, or 60 litters yearly.

How many sows and boars should we have in our nucleus to give us the required 5,000 boars annually?

We saw that the average boar produces 60 litters a year. Exceptionally good boars, however, are much more intensively exploited, and it is not excessive to make a good boar produce 200 litters per year.

If we take the average litter to be 8, this would give us 1,600 piglets per boar, 800 of which would be males. Let us suppose

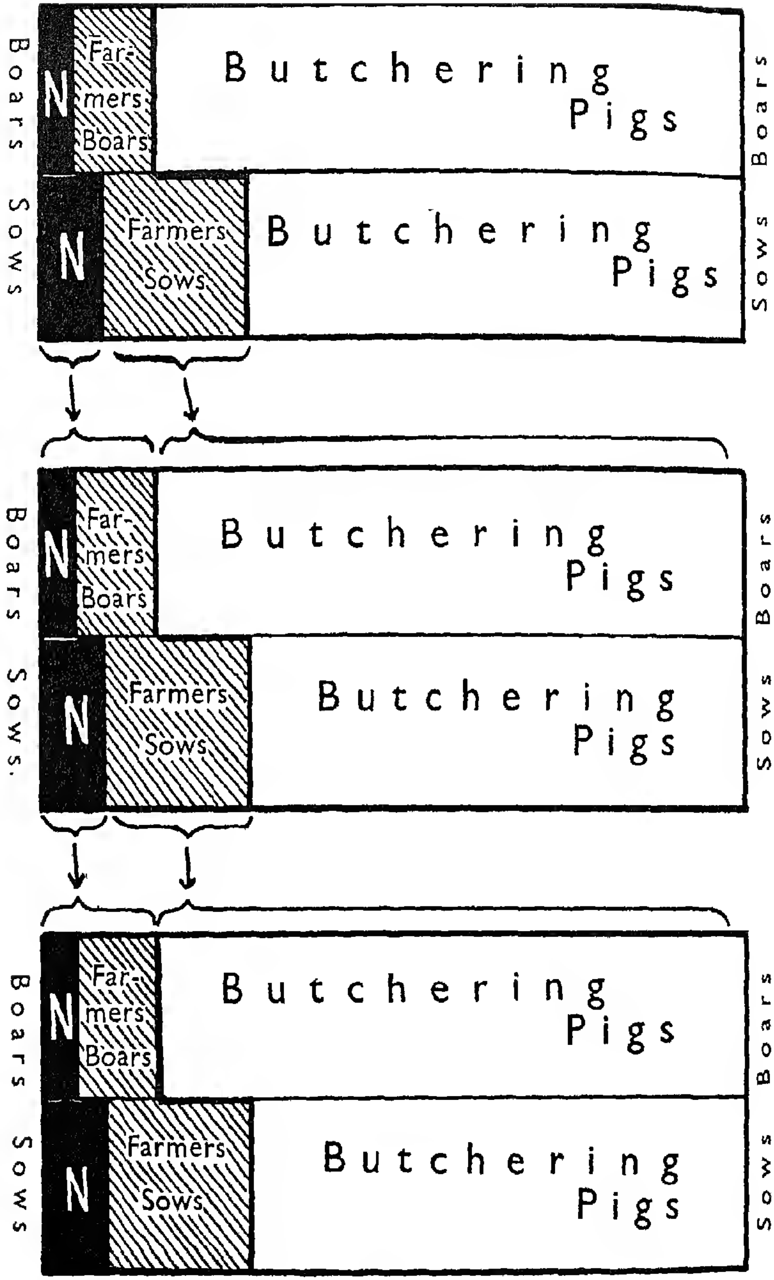
that we would only take 500 sons per boar, this would mean that we would want 10 boars in the nucleus, and 1,000 sows (2 litters each). Those 10 boars would be used on the average for three seasons each, so that it would be sufficient to add three or four boars to the nucleus every year.

These four boars must be proven sires, they must be proven before they are added to the nucleus. This means testing a number of boars to find four every year that are wholly reliable as breeders. At present a number of boars are found to produce aberrant young, they must be heterozygous for important genes, in other terms they carry "recessive lethals". It is obvious that no lethals are shown to be present in the genotype of a boar unless he is mated with heterozygous sows. For this reason it would be perfectly feasible to "test-mate" a boar with proven homozygous sows! To obviate this, we can test-mate our boars with virgin sows.

It is obvious that we want a good sample of every boar's offspring. Let us say that we test five entire litters, out of five young sows, approximately forty young piglets. In the first place we should look for lethals. Every time we find a piglet with atresia ani, or hernia, or any of the other recessive characters found in the breed, we can stop our testing and reject the father for our special purpose. When, however, forty perfectly growing piglets are born, we must test them for growing capacity and economic food consumption. In Holland and Germany numerous official testing stations have been built according to the Danish example. In Holland we have several of these stations, large enough to test 2,000 pigs a year. If we would utilize this apparatus, we could test 50 boars known to carry no lethals.

It is obvious that we can have no absolute guarantee that out of this number of boars tested (including the boars rejected for lethals this would mean testing about 150–200 boars) four would be really homozygous for every gene we want our pigs to have. Even if one or two of those boars were still heterozygous for a few genes, they would surely be homozygous for a very great number of the really valuable genes. If we restricted our selection of sires in the nucleus to such males only, this would mean that our nucleus would rapidly become more and more valuable, and the proportion of undesirable boars produced in the nucleus would become smaller and smaller from year to year.

This nucleus must be registered in a special herd-book made


Boars
N
Farmers Boars
Butchering Pigs
Boars
Sows
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Farmers Sows
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Sows

Fig. 22.

for the purpose. The animals of the nucleus would be in the hands of a number of pedigree breeders, and those breeders would be continually on the look-out for valuable, promising sons to test in order to have them accepted into the central nucleus herd.

It is obvious that the few owners of the ten "grandfathers" would have a monopoly of the production of service boars for the whole country, and for this reason it will be well worth while for the breeders to strive to find a few boars that are good enough to continue the nucleus.

If we make the regulation that only the sons of a few thoroughly-tested boars can be used for breeding, this does not mean that those sons will all be excellent breeders; but we are sure that, considered as a group, they must be much more valuable as breeders than the average boars that are used to-day. In the chapter on test-mating I calculated that the proportion of heterozygotes for any gene in a group is halved, when in one generation only homozygotes for that gene are used in one sex.

By concentrating the selection in a breed on a relatively small nucleus, the whole breed benefits from the purification of this nucleus. When we ensure that only sons of a few specially-tested sires are used for breeding, in two generations all the females in the breed have such a tested male as grandfather.

In fact, by establishing a small nucleus of very homozygous

Fig. 22.—Propagation in a population of pigs of one breed, under the *Nucleus Scheme* of selection. The butchering pigs of any generation are produced from the farmer's boars and sows of the preceding generation.

The farmer's boars and sows in every generation are the progeny of the stud-book sows (marked N) of the nucleus, mated to a very few highly-selected boars (marked N).

Those few grandfathers constituting the nucleus in any generation are selected by means of rigid progeny tests from among the male progeny of the N-groups. Only sons of tested boars of the nucleus group are allowed to breed at all.

Every pig in the breed is the grandchild of a boar in the nucleus. The selection of the nucleus males is based upon progeny-tests designed to find the few outstanding prepotent sires, free from lethals. The group of farmer's boars is carefully watched to find the few prepotent boars necessary to keep this nucleus up to the required number. To this end the apparatus of testing stations is fully used, to test real random samples of pigs from first litters of young sows, sired by promising farmer's boars.

All males produced by the farmer's boars and even by the highly prepotent nucleus sires before they have been officially recognized as such, are always castrated. The studbook is absolutely closed to the entrance of any animals not born from the boars of the nucleus group, in order to diminish the impurity and heterozygosity in the breed. The risks due to in-breeding are eliminated by admitting to the nucleus only such boars as produce no second-rate offspring of any kind.

males, we are "grading up" the breed to the level of these animals.

In different animals the nucleus scheme must be adapted to the peculiarities of the material. From our example we saw that in swine it is possible to have so many sons of proven sires that the annual production of approximately 2,000,000 pigs is sired only by such boars.

In poultry the large breeders have so many animals that they need not co-operate with other breeders in a nucleus scheme; each breeder can do the work for himself with his own birds. It has been found in practice that in poultry and ducks a nucleus of only one male in every generation is sufficiently large to produce all the males required on the farm. In other chapters I have described my system in detail. By comparing the progeny of a number of males, each group born at the same date, we find the male whose progeny scores highest in everything contributing to profit—number of eggs, weight of eggs, food consumption, mortality, etc. Only males from this one father are used on the farm, and among those young males one is chosen to be his father's successor, using the same system of choice. This system has proved a complete success with ducks as well as with poultry.

In the breeding of cattle, the herd-book officials in many countries have understood that it would be important to have a nucleus of the very best stock in the hands of the pedigree breeders, from which nucleus bulls would be furnished to the users.

The idea is sound, but the organization of the system is far from perfect. A geneticist, with a sufficient insight in animal breeding, can easily point out the faults in the system and the way in which it can be perfected. In general we can say that the chief faults of the system lie in wrong standards of perfection and in lack of concentration in matters of selection.

In other chapters I have treated of the standards of perfection and have pointed out the necessity of putting economic value far above show points.

At present in all countries the selection in cattle is scattered over much too wide a front. The thing we need is purification, reduction of variability, and the best way to obtain this goal is to concentrate the attention on a comparatively small nucleus in every breed. We have seen that in Holland we have a system of

"preferent" bulls. Such bulls are selected by a committee, who examine the way the bull has bred. At present far too much attention is given to the show points of the bull's daughters and not enough to profitable production; and no attempt is made to provide that the descendants examined shall constitute a true random sample of the bull's progeny.

The first step to be taken consists in improving this system of finding excellent bulls. As a matter of routine we will have to test the value of a great number of daughters, and the best way to do this is to examine a certain number, say fifteen daughters born from heifers, to obviate selection of dams. One of the easiest ways to make these daughters a random sample is to take the first fifteen daughters born from heifers. A system of compulsory milk-testing of all cows, such as Germany has, would facilitate matters, but it would not be necessary.

The first work can be done in the herd-book office, on paper records only. This narrows down the selection to relatively few bulls. In the regulations some method must be fixed to make it impossible for aberrant calves to disappear. In a black-and-white breed, the birth of a red-and-white calf should debar its father from further competition, and the same must be true of all lethals.

It is important to know how many bulls we really need in every generation in every breed. This directly depends upon the number of sons we can breed from one sire. The more young bulls we can produce from one proven preferent bull, the fewer of those "grandfathers" we need, and the stricter we can make our selection.

Several things must be taken into consideration. It takes about three years to prove a bull, and we can estimate the useful life of a proven "grandfather" to be about four years. This means that every year we only have to find one-fourth of the total number of proven bulls required.

It is not exceptional even now for a popular show bull to produce 200 calves a year, or 100 sons. In a country like Holland where 6,000 bulls are in use, we would need 600 "grandfathers" if these were mated normally. If we were to make use of artificial insemination, so that every service fertilized about five cows, we only need 120 bulls, and this means that we would only need to prove 30 homozygous excellent fathers every year. This is surely not excessive. With this number it would be

possible to prohibit the breeding from bulls that were not sired by the approved bulls of the breed.

As in swine, concentration of the selection upon a relatively small nucleus would result in a relatively rapid purification of this nucleus. We would establish an excellent breed within the breed, and the general breeding of cattle would become a sort of grading-up process of the whole cattle population by means of the few bulls in the pure nucleus.

It is evident that such a system would fit well into the work of the herd-books. The production of the general run of bulls would be in the hands of relatively few herd-book members, producing bulls would become a monopoly, and for this reason very profitable. It stands to reason that a Government that goes so far as to prohibit the use of bulls other than those bred from the few tested grandfathers has the duty of supervising the testing of those grandfathers. This can be done in co-operation with the herd-books.

When we leave the breeders to propose bulls for the progeny-tests, they can be relied upon to see that these are typical representatives of the breed. For the rest, it is obviously necessary to divorce the nucleus-system of breeding from show-point selection, as far as economically-useful animals are concerned. It should be repeated here, however, that the purification which results from taking a relatively small nucleus as the centre of every breed, from which breeding stock radiates out to the periphery, will automatically also result in fixing a visible "type" in the breed.

I know that some people are afraid of my nucleus scheme because of the in-breeding they think it involves. Most people have no clear conception of the reason why in-breeding causes the appearance of aberrant individuals. When once we realize that heterozygosis causes in-breeding troubles, it is clear that in the testing of males for unsuspected heterozygosis, we have a guarantee against such trouble. The breeders are free to introduce as many unrelated females in the herds, which have to produce the commercial males, as they think fit.

In sheep as in poultry, the larger breeders own a sufficient number of animals to take the selection into their own hands and to establish small nuclei of their own without any co-operation with fellow breeders. By comparing flocks of young stock, each bred from a separate male, breeders can find one or two

superior males in every generation to serve as a nucleus for the production of males in their general flocks.

In every species of polygamous domestic animals, this system of breeding by means of nuclei consists of a selection in the male line only. As a basis of selection the quality of the progeny of a number of males is compared, and where the females are the really productive animals in the breed, as in poultry and dairy cattle, the selection is in the main based upon the quality of the female progeny. While this is true, however, no mass selection is made between good and less excellent females within the groups. Even where the groups of daughters which have been compared to furnish a basis of selection of the respective fathers are taken as breeding stock to continue the nucleus as in poultry, no culling takes place in these groups.

Throughout the work one of the most important principles is the correct sampling of an animal's progeny. This is the point in which the usual systems of finding superlatively good breeding males have generally been deficient.

It does not seem to be common knowledge among breeders that the existence of very large numbers of animals in one breed is a great drawback, when we want to produce purity in regard to the most profitable genotype. The old system of encouraging the breeding of a great number of selected sires and females, as in the selectively-registering herd-books of continental Europe, leaves so many males breeding that there is scarcely any reduction in variability. The remedy is the establishment of a relatively small nucleus containing only a few males in every generation. Under those conditions a very strict selection is possible, so that only such males are used in the nucleus as have been shown to be homozygous for a great many important genes. Whereas in the ordinary course of things, prepotent sires are few and far between, so that their influence is swamped by that of sires of mediocre purity, in such nuclei nothing but prepotent sires are used, and they are used to great advantage.

The nucleus is kept as a separate "breed within the breed", a group with a rapidly-diminishing potential variability, and a rapidly-increasing average quality. Its main use is to produce enough males for the bulk of the breed.

Even in the nucleus system of utilizing prepotent sires there is a relation between progress and the total number of animals in the breed as a whole, simply because the number of males

required in the breed determines the number of males needed in any generation. The smaller the number of males needed, the fewer "grandfathers", and this means a stricter selection.

When we have to choose between continuing separate sections of a mass of related animals as separate breeds, or amalgamating them into one whole, we should keep those breeds separate wherever possible.

When Mr. van den Bosch declared as a result of many measurements, that all the Dutch black-and-white cattle belonged to one breed, this resulted in an amalgamation of many different strains, the cattle of the fat polders in the western part of Holland, the black-and-white sand-cattle, the cattle of the Zeeland islands, etc. We now realize that this has been a mistake from the point of view of a breeder interested in purifying the cattle of his district. There has been one exception in Holland: the province of Friesland has kept its own separate herd-book for black-and-white cattle. We must now realize that this separation is all to the good. The animals in the two herd-books should be kept apart as much as possible, as this will facilitate selection and purification. In Holland there are just now five breeds, two groups of black-and-white, one group of white-headed Groningen, one group of red-and-white, and a smallish group of belted cattle of excellent quality. It would be to the ultimate advantage of the farmers in that country, if the number of separate groups could be increased, either by the importation of additional breeds, or by the splitting up of existing herd-books into component parts.

Even in the largest groups, the establishing of a central nucleus in which prepotent sires are used to advantage is a method that will make progress towards purity possible, where progress without this system is almost impossible.

NOTES

This is Hagedoorn's main contribution to the theory of Animal Breeding. He defines the nucleus as follows:

"The nucleus is kept as a separate 'breed within the breed', a group with a rapidly-diminishing potential variability, and a rapidly-increasing average quality. Its main use is to produce enough males for the bulk of the breed."

It seems to me that in discussing this Nucleus Scheme of Breeding, there are two separate points to consider—first, its advisability, and second, its practicability—whether the scheme is or is not in itself a good thing, and if judged good, how best it could be implemented and applied.

Essentially, the Nucleus Scheme is one system of in-breeding, carrying with it all the advantages and disadvantages any such system must necessarily involve. Hagedoorn favoured in-breeding, believing as he did, that following upon a somewhat difficult period during which undesirable recessives were being discarded, breed purification and uniformity would finally result. He laid great stress upon the desirability of uniformity and has been criticized by other geneticists for doing so. Thus, in a review of the fifth edition of this book, it was stated:

"In its preoccupation with purity as a panacea the book is perhaps most out of touch with recent genetic thought." (G. Wiener in A.B.A., v.23, no. 958.)

Is it, however (and that might well prove more important), equally out of touch with future animal husbandry practice? In stating his farmers' ideal of what a farm animal should be, Hagedoorn wrote:

". . . he wants cattle or sheep or poultry that react in the same way to the same treatment—animals that start producing at the same time and that during production can be treated alike."

This definition of the ideal farm animal for production purposes seems to me to be even more applicable to the future than to the present. With the development of ever more intensive, fully mechanized and labour-saving methods of animal production, uniformity of stock in performance (although not necessarily in appearance) becomes a matter of the highest priority.

To what extent may in-breeding be expected to produce such desirable uniformity? According to one critic of Hagedoorn's, to a negligible extent, this critic's argument being that in his belief in the efficacy of in-breeding in producing uniformity, Hagedoorn fell into a fallacy, the fallacy being "that a great deal of the variation in most characters is not genetic" (J. M. Rendel in review of fourth ed. in A.B.A., 19, 2002). I am quite certain, however, that Hagedoorn was fully aware of the importance of variation attributable to environment. What he was immediately concerned with, however, was the reduction in that variability due to heredity, and in-breeding is, unquestionably, the best, if not the only, method of achieving such a reduction. Provided in-breeding were sufficiently close and environmental conditions standardized, I think it would be reasonable to expect the uniformity of reaction which Hagedoorn sought and to which he attached so much importance.

Even lacking the assistance of close in-breeding in producing genetic uniformity, the greater degree of uniformity in certain breeds is already to their advantage in competition with others. It is one reason, and an important one, for the expansion of the British Friesian at the expense of the Dairy Shorthorn. A good Dairy Shorthorn is every bit as good a milker as a good Friesian, but there are fewer good milking Dairy Shorthorns. As Hagedoorn emphasized, to the commercial farmer as distinct from the stud-breeder, uniformity of production is of much more importance than is occasional excellence. In fact, there would seem to be a good case in favour of Hagedoorn's "preoccupation with purity".

As Hagedoorn emphasized, because of the polygamous nature of farm

animals, genetic purity, if desirable, is most readily secured through the male, and the fewer males used, the more quickly genetic purity would be secured. As he himself wrote:

"The ideal in the nucleus herd must be to use as few males as possible," the reasons being that:

(a) *The fewer the males the stricter the selection, and*

(b) *The fewer the males the greater the reduction of variability in each succeeding generation.*

Hagedoorn wrote the first edition of his "Animal Breeding" *in 1939, and since that time the dramatic developments in A.I. and its techniques have raised the naturally polygamous nature of farm animals to the* n*th power. With the possibilities of A.I. as fully exploited as they are now in the British dairy industry, the practicability of securing genetic uniformity, rapidly and effectively, has been vastly increased. There is really very little difference between Hagedoorn's "Nucleus Scheme of Pedigree Breeding" and the scheme recently announced by the English Milk Marketing Board of using no more than 200 bulls to inseminate all the dairy cows of England and Wales, where pedigree breeders, presumably, will breed the bulls and the best of these bulls after progeny testing will be used to inseminate all the commercial milking cows in those countries. The final success of such a scheme depends upon the few males retained for breeding being in fact the best. Obviously the genotype of a sire used to inseminate many thousands of females should be subjected to the most searching exploration, and Hagedoorn, perhaps more than some others, realized the primary necessity of that search.*

Success also depends upon the validity of Hagedoorn's interpretation of what is often called "the apparent degeneration due to in-breeding", being, in fact, merely apparent and due to the easily understood hypothesis of undesirable recessive genes coming together in the homozygote. Is that, or is not that, all the "apparent degeneration" due to in-breeding involves? I doubt whether many modern geneticists would care to be entirely dogmatic on that subject.

In discussing the practical implementation of his Nucleus Scheme, Hagedoorn made the point that after the establishment of a nucleus group—

"The next step would be to make it obligatory to use only males produced from the nucleus group in the propagation of the breed."

Clearly, without some element of control, no nucleus breeding scheme of this nature, no matter where or by whom conducted, could be expected to have any very rapid or sustained effect upon the livestock of a country. In actual fact, that control must come to lie, eventually, in the hands of those who control insemination centres, since it is with them that rests the decision as to which sires will, and which will not, stand there. What should the controlling authority be, the Government, the Breed Societies, the commercial producers? Probably most suitably by an organization representing the commercial producers, such as the Milk Marketing Boards, already established in the dairy industry of this country.

Chapter Thirty-Three

Adaptability of Breeds and Pure-breeding Nuclei

Conditions in agriculture change: the demand changes. In some districts during a number of years it will pay best to produce beef, at other times milk. Some breeders make a very good business of raising pigs for the bacon factories, but others prefer to keep only a few hogs that can be profitably kept at home as a sort of savings bank for the family lard supply. The soil and situation of one man's farm will make it profitable to keep sheep for the early lamb trade, while in another district wool is very much more important. The availability of labour is one of the most important limiting factors that will decide whether a farmer will keep a flying herd or a self-contained breeding farm for meat or dairy purposes.

Our livestock must be adaptable. Does this mean that the ideal breed is a dual- or triple-purpose breed, in cattle, or swine, or sheep, or poultry? Theoretically it does, to a limited extent. The ideal dual-purpose animal is that one which, when treated in a certain way, will economically give us excellent returns in one way, but which, when differently treated, will fit into another scheme of exploitation. This, of course, can only be expected when the two purposes are not mutually exclusive. In many instances there seems to be no reason why excellence in one quality should not be compatible with excellence in some second quality. Why should we not have first-class wool on ewes that regularly produce first-class twins in February for the hot-house lamb trade? Why should we not have a pig that is of first-class bacon quality at twelve stone but that will grow into a mountain of lard later on?

The greatest difficulty in perfecting dual-purpose *breeds* lies in

the very fact that the two qualities esteemed *are* physiologically compatible! This means that the genes that will help to produce excellence in one respect and those that are desirable in the other are transmitted quite independently. This will make it very much more difficult to select for both purposes at the same time than it would be to concentrate our efforts upon one of them, and leave the rest to chance. As long as the breed is highly variable, it will always be possible to find occasional individuals that happen to combine perfect beauty with perfect production, or a high yield of eggs or milk with meat. Further, the fact that such individuals do occur keeps encouraging the amateurs of that breed in their belief that they are a long way towards producing a "fixed breed" that will breed pure for all the desirable qualities.

The perfect way to increase our chance of producing the ideal individual for advertising purposes is cross-breeding, mostly within the breed. It is generally called "combining the most valuable bloodlines", or "corrective mating". The method is highly successful and can be recommended to breeders who want to make a reputation as breeders of outstanding animals at the shows and sales. From the standpoint of economic agriculture, however, it is deplorable—there is no question about that. It would certainly be possible in many instances to combine a number of valuable qualities in one family group, in one breed, if a determined breeder or group of breeders would take the trouble and could afford the expense entailed, to breed a largish, self-contained herd with the aid of the very best methods. In practice, the efforts of well-meaning breeders are wasted because they are not concentrated, so that all the work done really amounts to shilly-shallying back and forth between some more milk and some more beef, between some more eggs and better shape of comb or better eye colour to please the "handling" inspectors.

Adaptation of our domestic animals to different levels of agriculture, and to changing aims, cannot be economically attained by any method of keeping one breed variable. I concede that in a very variable breed like the Shorthorn it is quite possible for a farmer who enjoys marketing, to build up a profitable herd of milking cattle by a sustained policy of buying in likely-looking cows, and trading them off again when they are disappointing. The same possibility more or less applies to some breeds of

utility poultry and certainly to sheep. This, however, is after all a wasteful process. It means that in several respects the breed is not only variable, but definitely unreliable. The average quality is apt to be too low, and in many respects every important quality will vary so that we have a few excellent beasts, a great majority of mediocre value and some obvious culls. One individual horse buyer may pick out a few excellent head of horses from a very variable lot, but in any animal that has to be used in a group it gives a lot of unnecessary bother to fit the diet and treatment to each individual ewe or cow. It is much preferable if we can be reasonably sure that every animal born in the herd will respond well to one universal mode of treatment that gives us the optimum profit from the group.

One disadvantage of a very pure group is that if conditions change, the breed may not fit those conditions. At first sight it seems obvious that in this respect a variable lot will include a few animals that will happen to fit the new conditions, so that the breed may be changed to fit those new requirements. If we examine this position, however, both from a scientific angle and from actual examples, we shall see that this is a hopelessly difficult and slow business! Even if we find a few animals that may fit into our new conditions, we cannot in the least rely upon the way they will behave as breeding-stock. In other words, when we need a group of animals for a special set of conditions, or in a certain system of agriculture, we want to be certain to obtain them without too much delay.

This is where it is an advantage to have a great number of different pure breeds. Most of our breeds of cattle, ponies and sheep were local breeds originally, adapted by a long-continued process of conscious and natural selection to the conditions of agriculture that obtain in the region where they are kept. As explained elsewhere (p. 107) this adaptation may make some breeds of dwarfs live in adverse conditions where none of the bigger breeds could survive—on very rich farms we can keep some breeds of cattle or horses with profit, whereas those same breeds would be unprofitable when we would try farming with them on some hill farms. Where the winters are exceptionally severe we may get our profit easier from specially adapted breeds, and wholly different breeds of cattle or sheep are required in semi-tropical regions with too much sunlight.

In crop production, careful experimentation to find the right

varieties for special soils and in certain combinations and rotations gives our farmers very reliable data, and of course those varieties breed very true, even when there are only minute differences between them.

In the breeding of our farm animals we know too little about the quality and the adaptability of the various breeds. We still often hear that it does not matter which breed or which hybrid one starts with, they are all variable, they all contain excellent individuals, it is a matter of strain and not of breed. This is a gross exaggeration, and all we can say is that it is very wasteful of material and energy to leave the choice of our animal breeds to a slow method of trial and error, and to the influence of propaganda by the pedigree breeders and their organizations.

When we look around us, we see how quickly one breed can be changed into another, when we find this second breed is better adapted, by a process of grading (continued back-crossing). Some pedigree Friesian or Guernsey herds were pedigree Shorthorn herds five cow generations ago, both in Britain and overseas. Even for this we need reliable, pure-breeding bulls. The same is true for all those instances in which first-generation stores (cattle or sheep), first-generation hybrid poultry or cross-bred swine are continually produced because they have been proved to be very profitable. For this we do not want variable "plastic" breeds, but on the contrary we want very pure breeding-stock that can be relied upon, so that the males available for our purpose will produce just the kind of young stock we need.

The obvious method is the one that is so well known in the breeding of plants—in-bred, pure-bred highly-homozygous groups in every breed that can be looked upon as nuclei of highly-bred homozygous stock. The concentration of quality and purity in relatively small, intensely-selected nucleus herds or flocks is very much more economical than the scattering of effort over a great number of pedigree herds in the hands of hundreds of owners who may be continually selling out or (what is worse) buying in breeding-stock they know very little about. With our present improved methods of heightening the proportion of females to males, it is really astonishing to see how very few really first-class males are needed to continue each breed, and to father the young stock that will be used for utility crosses.

It is quite possible that in such animals as sheep, swine and cattle too many breeds exist in the sense that two or more of

them are simply differently coloured duplicates, or at least that often several breeds are adapted to absolutely the same sort of environment and agricultural conditions (although in our present absence of good objective breed comparisons it is not easy to decide this). This, however, is certain—we need a good many and we want at least one excellent and pure nucleus herd in every breed, if we want to attain a state of things where farmers will have herds rather than collections of beasts.

NOTES

After a discussion of the advantages and disadvantages of dual-purpose versus single-purpose breeds of livestock, Hagedoorn comes down very strongly on the side of single-purpose breeds specially bred and managed for the most efficient yield of one particular product, be that product milk or beef, mutton or wool, eggs or table chicken, but in no case both. Is that preference merely one other example of Hagedoorn's passion for purity or is it more sensibly based on factors of genuine economic importance? I think it is the latter, for Hagedoorn wrote:

". . . in any animal that has to be used in a group it gives a lot of unnecessary bother to fit the diet and treatment to each individual ewe or cow. It is much preferable if we can be reasonably sure that every animal born in the herd will respond well to one universal mode of treatment that gives us the optimum profit from the group."

That statement is entirely true and is likely to become of progressively greater importance the more labour-saving and mechanical techniques extend into the practice of animal husbandry.

One theoretical disadvantage of complete uniformity or homozygosity in any breed is that while marketing conditions might change, the breed couldn't. Hagedoorn recognized that difficulty. His solution, however, that it is "an advantage to have a great number of different pure breeds" so that to every new need some breed would be found to fit is not one likely to meet with general acceptance. Who, except for pure fancy, would maintain a breed on the off-chance that its particular productive qualities would fit in with some future and unforeseen market?

Chapter Thirty-Four

Government Activity

There are two wholly different reasons for the Government of a country to want to have an influence on animal breeding and animal production. In the first place the Government may help the farmers to get more profitable animal stocks, and for this reason it may help those breeders who work towards such a goal.

In a few instances, however, the Government of a country may want to influence animal breeding, not so much in order to help the breeders or the users of the stock, but to regulate the supply of animals of certain kinds, or the supply of their products.

The most obvious case was that of the breeding of army horses. In some countries the sort of horse needed for cavalry remounts was bred in sufficient quantities. This was especially true in countries where fox-hunting survived. In many countries, however, farmers tended to breed both heavy draught horses for the heavy work of the farm, and quick, active ponies for light transportation, but not the sort of horse the cavalry wanted. From the standpoint of the army the ideal was to have a constant supply of such horses, enough of them to select the relatively few riding-horses needed. As a matter of fact, from the farmer's standpoint, the number of horses needed for this purpose did not make it economically justifiable to breed such horses at all. In practice, however, it was found that the expenditure of a very little money in subsidies to the owners of the right type of stallions was sufficient to foist the required type of horse upon the horse-breeders. Farmers in most countries are poor economists, and arithmetic is not their strong point. A very effective trick was

that of providing for compulsory licences for stud-stallions, especially if the Government could appoint the judges.

On paper, a licensing system for stallions and even bulls reads very well, but in practice I have not yet met an instance where it could be said to work out satisfactorily, or in the interest of agriculture. The reason seems to be that the judging of stallions or bulls is done on lines that were deemed wholly admirable around 1890, but which we now recognize as wholly inefficient and often wrong.

While it must be said that it was the good right of the army authorities to provide for a continuous supply of the right sort of horses with as little expenditure as possible, we must recognize that such a system of small subsidies, destined to foist an unprofitable kind of horse upon agriculture, was not in the interest of the farmers.

Several instances are on record where the Government of a country has decreed measures intended to ward off some crisis in the proportion of supply and demand. The Governments of Germany and Holland have done quite a lot along those lines. The result has very often been lamentably bad compared with the excellent intention. One example is the regulation of the numbers of milk cattle and of poultry and swine in Holland. An elaborate system of licences was instituted in Holland restricting the number of calves that the farmers are allowed to raise. The object was a restriction of milk production, to protect the price of milk and milk products. The result in this one instance has been that the farmers, the majority of whom have pasture exclusively, so that they must have a certain number of cows if they are to farm without loss, have kept their cows to a higher average age, instead of substituting heifers for aged cows, and the result has been a marked *increase* of milk production, as could have been predicted. The regulations governing the breeding and selection of poultry, and the breeding of swine have given rise to a top-heavy bureaucracy, and an unbelievable amount of red tape! One thing stands out clearly from the experience in Germany and Holland with Government regulation of animal breeding and production, namely, that on the whole it is undesirable from the standpoint of agriculture. The chief beneficiaries of such a system are the army of small inspectors. On the whole it is preferable that the breeders and farmers themselves co-operate to regulate their industry.

There are many different ways in which the Government may help the farmers to get more profitable stock, and to get the utmost profit out of the animals used. Roughly, we may divide this activity into different categories. In the first place, in different phases of animal breeding experimentation is necessary, and the State may take the risks and cost of this experimentation rather than let them fall on those breeders who are most energetic. Secondly, the Government may employ well-trained public servants, able to give help and co-operation where necessary. Thirdly, the State may provide instruction for farmers and future farm advisers. Finally, the State may directly regulate and supervise certain activities of the breeders, the work of herd-books, bull-testing, licensing of studs, etc.

According to my way of thinking experimentation comes first. It is not logical that individual farmers and breeders should bear the cost and take the risks of experimentation. It has repeatedly been found that breeds developed in foreign countries are better than those in a given country, and it is often worth while to import a number of animals of a foreign breed in order to test them out fully. Cross-breeding experiments, designed to find profitable combinations of breeds for making first-generation hybrids, cost money. In many instances there exist preconceived notions about correlations between real value and external characters that ought to be tried out experimentally. Nobody is likely to profit immediately from the result of such experiments, and for this reason no single breeder will undertake them. Systems of selection must be tried out experimentally on a sufficiently extensive scale, but again, such work should not be loaded on the shoulders of private individuals. Every country should have a well-subsidized Institute of Applied Genetics, or at least an Institute for Animal Breeding, where experimental work having a direct bearing upon practical animal breeding can be undertaken by trained genetical investigators, who have a thorough working knowledge of practical animal breeding on the farm.

Such an institute would provide an excellent background for public servants, who have to be the liaison officers between the practical breeders and the science of genetics. It is not enough that men of this type should be well trained; they should keep in touch both with agriculture and with science, and should be able to work out their problems experimentally. My own experi-

ence with men of this type in several countries is that, without this background, and without facilities for experimental work, they soon crystallize, substituting fixed opinions for knowledge or for the healthy doubt that is engendered by doing experimental work; they become set in their ways, stop reading and studying and so may become a real menace to progress. Having had considerable personal practical experience of advising breeders and of co-operating with them in their problems, I know that in a great many instances experimentation under suitable guidance is indicated, and positive definite advice is impossible to give.

The teaching of genetics and animal breeding is of extreme importance. The enormous progress in animal breeding in America compared with the comparative stagnation in Western Europe is closely paralleled by the way genetics, and especially applied genetics, is taught at the Universities. From personal experience in teaching genetics and applied genetics I have learned among other things that to teach genetics one should be engaged in helping to build the science. To teach applied genetics one should have considerable personal practical experience in producing new kinds of plants and new breeds of animals; to teach animal breeding from textbooks and from a fund of set opinions gathered from other people's books is worse than wrong. Students should be encouraged to devise and perform experiments of their own, they should do some selection work themselves, and they should be encouraged to read and discuss even those novel viewpoints that seem heresies to the teachers. Some seats of learning where animal breeding is taught are hotbeds of conservatism, where the men responsible for the teaching seem to believe that the old ideas are good enough for them and will last their time anyhow.

In my own experience (gathered in very many countries) it has often happened that to get the farmers to adopt logical, rational methods of selecting economically important animals one has had to go over the heads of the official authorities who are opposed to anything contrary to what they have been led to believe to be eternal truth. The fault lies mainly in lack of facilities for experiment. The farmers are in touch with reality, and baseless but plausible sounding theories have small hold upon them—they are willing to try everything once. Some of the older official authorities, however, who have never had occasion to do

much experimentation, and who have therefore fallen into a rut and have accepted the opinions generally held in the days of their youth, are thoroughly shaken up and disagreeably surprised whenever new facts disprove their pet theories. Men of this type can do a very great deal of harm when the training of the new generation of farm advisers is put into their hands.

Lastly, I spoke of the direct regulation and supervision of animal breeding. The Government can assist or finance the herd-books, and it can see to the licensing of bulls and other sires, etc. The more I see of direct interference with animal breeding by Governments the less I like it. When a system of Government control in matters of animal breeding is started along the lines thoroughly approved by the present generation of breeders, it may work excellently for a time. In Canada the registration of animals and the keeping of herd-books are exclusively in the hands of the Government. I have seen this scheme in operation and I must say I admire it: and yet I think in the long run such work should not be in the hands of public servants who are neither breeders nor geneticists. Such men as a body must by the nature of their training and of their calling be conservative, and impervious to what newer facts and new experiments teach us.

I would except registration. The idea of giving animal registration into the hands of unbiased and impartial men is excellent, so long as this registration does not entail selection. I have repeatedly advocated obligatory milk-testing of all cows in Holland, instead of the 40 per cent. in some counties. The compilation of data by disinterested men should be thorough, but the selection based upon these data should always be left to the breeders, to the users of the animals.

The question whether our present usual sort of herd-books, even in economically useful breeds, can be considered to be of benefit to agriculture is a debatable one. I for one do not think they are of public benefit, and I think they ought not to be subsidized by the Government. The herd-books, especially those having selective registration, are established for the benefit of the members, who can get more money for breeding stock with, than for animals without, official papers.

Nearly all the herd-books select animals for wholly irrelevant points, which have nothing to do with real economic value. Most herd-books nowadays are taking economic value into

account, mostly in a half-hearted way, and secondary to beauty. This is doubtless as it should be in a corporation of men who earn their money as breeders by the sale of breeding stock. From a standpoint of public utility, however, the aim of animal breeding is not the sale of breeding stock, but the production of profitable animals for agriculture, animals of the right quality to make them fit in a balanced production-scheme.

For the Government to countenance the work of the herd-books by subsidies is wrong for several reasons. The sooner the public recognize that the showing of agricultural animals and the selection of such animals for show points is only a game that should not be taken seriously by breeders who want profitable animals, because it only slows down the really useful work, the better. *Anything that helps to keep alive the idea that the judging of individual animals has any practical importance for agriculture is wrong.*

It has been mentioned earlier that there was a time when in America beauty contests for prize ears of maize were held at the agricultural shows. A committee of judges solemnly conferred the prizes for the ears with the ideal shape. Breeders of corn now remember this tomfoolery as a silly, comparatively harmless game. It cannot, however, be said that animal breeders in general recognize that the judging of fat bulls at the agricultural shows is very much like the judging of ears of corn, and has just as little to do with breeding profitable cattle as the show-ear game had with the breeding of profitable strains of maize. Subsidizing the cattle shows is just as bad as subsidizing the corn-ear contests would be, if either of those two things were held up as of value to agriculture.

The licensing of stallions and bulls by the Government could be made into something of the utmost importance to animal breeding. As it is now done in Western Europe it is little more than a farce. What it amounts to at present is the licensing of good-looking "pure-bred" beasts, whose value for breeding is almost entirely speculative. In other chapters I have tried to set forth how this sort of thing could be done in a way that would make it useful.

NOTES

"The more I see of direct interference with animal breeding by Governments the less I like it."

"As it is now done in Western Europe it is little more than a farce."

"The chief beneficiaries of such a system are the army of small inspectors."

These three short quotations suffice to show what Hagedoorn thought of the well-meant efforts of Government Departments to supervize and regulate animal breeding in the presumed interests of national agriculture. Personally, I subscribe whole-heartedly to everything he wrote on this subject. There is no need for me to say any more.

On the other hand, while Hagedoorn was very much in favour of Animal Breeding and Research Organizations being under Government financial control, I am very much more sceptical. The conclusions based on research at such Institutions become "official" conclusions, yet such conclusions although "official" may be entirely wrong.

Chapter Thirty-Five

Artificial Insemination

In all our domestic animals the male, at every copulation, ejects an enormous number of spermatozoa, a number greatly in excess of the eggs to be fertilized. The exception is that of the honey-bee, every queen-bee being fertilized only once during her lifetime, the sperm being kept alive in her *receptaculum seminis* to fertilize the eggs during a number of years.

Every egg in our animals and birds requires only one sperm for its fertilization. The chances of something going wrong between copulation and fertilization of the eggs are so considerable that, in order to be reasonably sure of fertilization, a great many sperms have to be introduced to the spot where the ripe egg is descending from the ovary, as can be seen from experiments in which the spermatic fluid containing the sperm is greatly diluted. It is certain, however, that only a small portion of the semen commonly ejected at each copulation is sufficient to fertilize the egg or eggs present.

If, therefore, we can intercept the sperm at, or soon after a mating, we are able to use this sperm to impregnate several females, and this is the principle upon which artificial insemination depends.

This is not the place to give an extensive treatise of the methods and technique employed. Very clear special treatises have been published, mostly in Russian, of which some have been translated in other languages, including English. In general terms, the method employed consists of obtaining the sperm from the male, of storing it when necessary, diluting it where required, and finally of introducing it into the matrix or the oviduct of the female at the right moment.

In the larger mammals the sperm is generally obtained by

diverting the male's copulatory organ at the moment of mating, and gathering the fluid in a rubber receptacle. In dogs and in poultry it is relatively very easy to obtain a quantity of sperm by just pressing slightly on definite points, in cocks and drakes near the hip. It is important that no metal shall come in contact with the sperm. At low temperatures the sperm can be kept alive for a long time. Already before the Second War Hammond had shipped a ram's sperm from England to Poland, where a few ewes have produced lambs from it.

There are two objects in employing artificial insemination. The first one, which does not further concern us, lies in overcoming certain causes of sterility in the larger mammals. Many cows that do not "take", when mated in the ordinary way, are perfectly fertile when the sperm is brought through the vagina into the cervix, and the same is true for some mares.

The chief reason for using the method, however, and the one that concerns us in this book, is the possibility of impregnating very many more females with the sperm of one male, than would be possible in the usual way. An example is the breeding of cheap native ewes in Eastern Europe to very good, but very expensive rams of the Karakul breed, in order to produce a crop of fur lambs. By using artificial insemination the breeder needs only to buy one ram, where twenty would hardly be sufficient if left to mate with the herds naturally. In backward countries, where it is desired to grade-up enormous numbers of cattle into some superior breed, the method is of very great importance. (See "Breeding Special Groups of Animals".)

It is often supposed that in our own countries, where breeds of cattle, horses, sheep and swine have been selected for a long time, the method of artificial insemination is of no great importance, because there is no dearth of superior male breeding stock. This argument, however, is not of very great value.

In countries where the breeding of cattle is furthest advanced, in Denmark and in America, it has been shown conclusively that bulls and boars that father excellent stock, differ considerably in homozygosity. When, as in England, Holland and Germany, the interest centres around the excellent daughters of a sire, and because bull-testing is still considered as a novelty, not much attention is given to the mediocre and inferior stock a male produces; breeders do not fully realize the enormous importance of using for breeding only those sires that are

homozygous for most of the important hereditary factors, and that for this reason produce offspring of a very high average level of quality.

When progeny-testing of bulls and boars and cocks and rams has gone on for some time, breeders realize that, even in the so-called highly-bred animals, very few sires produce nothing but valuable offspring. Such sires exist, but they are rare; the common run of so-called excellent sires produce a good many offspring of inferior quality.

When by means of good methods of registration and study a single one of these thoroughly excellent sires has been discovered, it is highly desirable that this sire shall be employed for breeding as much as possible.

The utilization of a few really homozygous sires by means of artificial insemination has never, as far as I know, been fully thought out. The possibilities in this field are very great indeed.

In the first place, the very few really great sires are at present used in comparatively small herds. Sometimes a few females from outside the herd are bred to such a sire, but the fees are generally very high. Where farmers co-operate in the ownership of a bull or a boar, the number of females owned by the corporation quickly mounts to a number that necessitates the use of at least two sires, often of three.

It is clear that of three bulls owned by a breeders' corporation one is better than the others, and it would be an obvious advantage if, by means of artificial insemination, this best one of the three could do all the work. A further point is that for the price of the three bulls one of superior quality could have been bought, and this again helps to make the method economically sound.

The technique of sperm-dilution and the keeping of sperm is gradually being worked out and improved, so that the number of cows that can be fertilized with the sperm from one mating is gradually being extended. It is obvious that it is only a matter of organization to make it possible for the owner of one excellent bull to extend the services of this bull over half a county instead of over the owners of twenty cows. The cost of one impregnation can be considerably lowered, and yet the amount of fees brought in can be greatly augmented.

It is true that, in order to find one proven bull homozygous

for a very great number of economically-important hereditary factors, a great number of young bulls must be tried, among which the large majority produce a mixture of good, bad and indifferent offspring. This, however, does not condemn the system of proving sires, for under the usual system in England and on the Continent the breeding of untested sires is almost exclusively the rule. By spreading the influence of a few highly desirable sires, the proportion of offspring produced by tested sires, as compared with that produced by untested sires, can be greatly improved.

Under the present system most bulls used are wholly untested, while a few thoroughly tested excellent bulls are very sparingly used; but the influence of the tested bulls is relatively slight, and the great majority of animals born in every breed are the product of untried, possibly very heterozygous sires.

When we remember that not all females born are necessary for the continuation of the breed, even in cattle where the fertility is relatively low, it can be seen that it would not be difficult at all to reach a state of things in which the number of females produced by untried males (or by males that were tried and pronounced unreliable) that would be bred from, could be made very small in proportion to the number of females from proven, excellent sires.

Too often we hear the argument that the proving of excellent sires and the multiplication of their influence upon the breed by means of artificial insemination would be dangerous, because of the greater in-breeding such systems would entail. The argument shows a deplorable lack of insight into the nature of possible degeneration due to in-breeding. In-breeding, as we have discussed in another chapter, *is* harmful where the related animals mated are heterozygous for the same inherited factors. The object of bull-testing and progeny-testing in general, however, is the finding of sires homozygous for many important genes, and if the work is well done the wrong sort of sires have very little chance of being considered good.

The fear of the in-breeding that must result from the extensive use of proven sires, made possible by artificial insemination, can be understood when we see how often the most highly-approved sires disappoint. I know several instances of bulls and stallions—widely-known and much-advertised champions—that take all the important honours at the shows, that are very poor sires

from a breeder's standpoint. Obviously it would be very unwise to use such animals in a system of breeding based upon the employment of only a very few sires!

I have repeatedly been asked by breeders who know some thoroughly bad bulls with glowing reputations, what would happen if a proven bull that had produced thousands of calves should turn out to be "a real bad one".

The question answers itself: there is only one system of making sure that a boar or a stallion or a bull will be a great success as a stock-getter, namely, this system of evaluating him only according to the very thing we want him for, the quality of his descendants. This system of estimating the value of a sire is not only wholly fool-proof, but it is the only fool-proof system. No sire should ever be used to any great extent until we know what the quality of his descendants is.

When, as in the twenty years that lie just behind us, a bull or a stallion is widely advertised as a stud animal on the basis of his individual show points, or on that of his mother's record, and serves a great number of females before we know anything about his real breeding value, disappointments must be common.

Although in thoroughly conservative countries it sometimes appears as if the system of breeding animals according to type and pedigree is still firmly entrenched, its foundations have been thoroughly weakened in different spots. As soon as the issue is clearly seen to be one between the gentlemen-farmers, who earn their money by selling good-looking breeding stock (and therefore have to support the system of showing and judging according to show points), and real farmers, users of the animals, who must make their money by producing milk economically and by selling butter, meat and eggs, then the farmers are bound to win and the antiquated system based on false values will have to go to the wall. The widespread interest in bull-proving schemes is the thin end of the wedge; as soon as the farmers understand that there is a system that bases the recommendation of sires upon facts instead of upon speculation, they will lose interest in beautiful untried bulls and stallions of speculative value, and will want their animals to be mated with sires of which it is surely known that all the offspring are valuable.

For this reason progeny-testing and artificial insemination must progress hand in hand. We know that many good-looking

stud animals are very disappointing sires, and it is certain that only a few sires tried are superior in every respect, so that we may safely say that the fewer sires are used in every generation, the quicker the weeding out of inferior stock will progress.

As is explained more fully in other chapters, polygamy can be made to help very much in selecting animals and birds. It suffices for all the animals of one sex used for breeding to be homozygous for any gene to halve the percentage of heterozygotes for that gene still present in the population. The more we reduce the number of breeding animals of one sex, the easier will it be to see that they are all homozygous for the most valuable genes. By utilizing the method of artificial insemination we greatly reduce the number of males necessary per group of females, in fact, we can say we make the fullest possible use of the polygamy of our animals.

With regard to poultry Miss Heringa and I have worked out a method of mating fowls which is in some respects very similar to artificial insemination. When a cock is left to run with a number of females, he mates more often than is necessary for a good percentage of fertile eggs. We found that one mating in ten days was ample. As a cock in good health generally mates more than twenty times a day, this means that we need only to keep one cock to about 200 females, provided we ensure that he mates with every hen only about once in ten days. To accomplish this, we must have recourse to trap-nests. We need an ordinary calendar laying-list, on which we mark down the ring numbers of the trapped hens. Only, instead of releasing each hen immediately, we hold her until we look on the list when she has been mated the last time. We make a special mark on the given day in the appropriate space on the list, e.g. with coloured pencil. When we notice the hen has been mated within a week to nine days we release her; if, however, the last mating has taken place ten or more days ago, we give her a mating.

The male is penned separately, and he is trained to tread each hen immediately she is introduced in his pen. The hen is not released, but held for the cock to tread. By this means it is possible to get a much higher percentage of fertile eggs, probably because some hens, when running in a crowded pen, are able to get away from the attentions of the male, so that they never or mate. The system works with ducks as well as with nly it takes more care and time. With both kinds of

birds it is an excellent system to employ when we possess a proven breeding male of very high quality from which we desire to obtain as many offspring as possible.

Artificial insemination of some kind is not only indicated where we want to obtain very many offspring from one male, but also when for any reason normal mating is difficult to obtain or is ineffective.* We have already treated of the use of this method to overcome sterility in some instances. Another use of the method is seen in cross-breeding animals of different kind which mate with difficulty or not at all. Before the First War I employed artificial insemination in mating Leghorn male to Game bantam hens and vice versa, the unequal size of the parent birds making normal mating impossible. Both in animals and birds hybridization between species is very difficult, but relatively easy by means of artificial insemination. Hybrid embryos between chickens and turkeys have been obtained in this way in Russia and America. Anyone who has ever seen the exasperating and often grotesque difficulties encountered in the breeding of mules will concede that artificial insemination of mares with donkey sperm, obtained by mating a jack to his own jennets, is a good way around this obstacle!

In the breeding of those fish whose eggs are fertilized after being laid, artificial insemination does not really differ from the ordinary process, and for this reason this method has been in use in fish hatcheries from immemorial times.

In the breeding of honey-bees, the one mating of each young queen takes place during a nuptial flight, and for this reason it is very difficult to obtain controlled matings otherwise than by isolating the colonies on islands. Several methods of artificial insemination have been proposed and tried. See under Honey-bee. One of the best methods uses a sort of hand-mating system in which the drone furnishing the sperm has been killed first.

Some animals, like the ferret and the rabbit, do not ovulate spontaneously, so that without copulation no success can be expected from the introduction of sperm into the cervix of the female. In these animals it is necessary to use vasectomized males to copulate with the females they are unable to fertilize, in order to prepare them for artificial fertilization.

* A. I. is quite feasible in birds.

Chapter Thirty-Six

Breeding for the Shows

In other chapters we have discussed the influence of the shows upon the breeding of animals and birds that are mainly kept for economic purposes. We have seen that even on such animals the show-ring has a very great influence and I have repeatedly pointed out that this state of things almost always counteracts progress in the breeding of economically valuable animals. With poultry the breeding of utility stock has been freed from the influence of showyard standards, so that the selection of good poultry is not shackled by show ideals. This has not stopped the breeding of poultry for the shows and in all the purely utility breeds, the breeding of special families of those same breeds, purely on lines dictated by beauty and fashion, has gone on as before.

Although as a geneticist I deplore the fact that in the selection of good, profitable animals the showyard ideals have made things unnecessarily difficult, I recognize that breeding animals for the shows is not only a hobby, but a paying industry for those who understand it and who make a success of it. This is especially true when the animals have some economic value. There is certainly more money in breeding draught-horses or sheep or pigs for the shows than there is in raising those animals for the ordinary market.

Breeding animals for the shows is a very peculiar business, because of the fact that it is wholly competitive. Whereas the breeder of utility sheep or utility pigs produces something that has a certain market value, which is not changed very much even if ten of his neighbours start in with him to raise the same sort of sheep or hogs, breeding animals for the shows can only pay the man who succeeds in producing such stock as is pro-

nounced by the judges of the moment to be the most beautiful and the most fashionable.

This is one of the reasons why breeding show animals is very much more difficult than breeding excellent animals for use. If a man succeeds in purifying a strain of Campbell ducks until they lay so many eggs for a given amount of food that they are very profitable to keep, his customers will soon recognize the quality of his birds, and his business will prosper accordingly. This is especially true in such countries as Holland where show-room standards have been thrown overboard completely in this particular breed of utility ducks.

A breeder of the same sort of ducks in England is up against the fact that here the divorce between utility standards and show-room standards is not yet complete, so that in his selection he has to reject a certain number of his very best birds because they show too much or too little white, or have the wrong shade of bill, but even he is mostly concerned with real economic value, and therefore with an unchanging standard of quality.

The show breeder of Khaki Campbell ducks, however, must not only produce ducks that conform to a very rigid standard of beauty, but even his most beautiful birds are not worth anything unless they are just a little more beautiful than his competitor's birds at the shows. Also, this standard of beauty is not fixed for him; it slowly changes, so that he has to revise his own standards according to which he selects his breeding birds.

Another reason why breeding for the shows is so much more difficult than breeding for the market lies in the fact that different judges have different ideals of beauty. The breeder of utility animals has to produce the sort of stock that under optimum environmental conditions pays best to raise. In order to win at a show, however, the breeder must first produce his beast; next he must fatten it up, or trim or train it until its condition accords with the fancy of the moment; and, thirdly, he has to send it to the show where he knows the judge favours this particular kind of animal. Whereas the utility breeder is chiefly concerned in producing animals or birds with the correct set of inherited factors, the show breeder must study the effect of environmental factors in the development of his animals, and he must be constantly on the look-out for the way the fancy develops, which animals win under certain judges, which animals under others.

The effect of environmental developmental factors on the quality of a show animal is very much more important in some classes of animals than in others. In such birds as pigeons and chickens correct genotype and the choice of the correct judge are the main things, and very little can be done to improve the appearance of the birds for show purposes.

In certain breeds of dogs, show preparation is much more important; the fashionable winners in some breeds owe their success almost as much to the art of the trimmer, who models them according to the latest taste, as to the art of the breeder, and almost the same can be said for some breeds of sheep.

The ultimate importance of environmental factors, however, is seen in the showing of bulls. Unless a young bull, intended for the show, is fed in a certain definite way from an early age, he will never be worth much at the shows. A good cattle breeder who understands the showing of bulls can safely let three or four farmer breeders take the pick of his bull calves, and still be reasonably sure that those bull calves will never become serious competitors of the one or two he has left over, when he decides to make show bulls of them.

Anyone who intends to take up the breeding of show animals or show birds as a hobby or as a means of earning money must first understand the peculiar nature of the business on which he embarks. In showing one individual bird or animal, nothing counts in success but the appearance of that individual at the moment it is shown. Anyone breeding for the shows must always bear this in mind. In fact, breeding for the shows and showing are two comparatively unrelated things. In many variable breeds, breeding is not really the most economical or the surest way of success at the shows. Someone who possesses a thorough knowledge of what the judges like at the moment can often pick up a few winners in unexpected places. When the Barnevelder fowl was at the height of its fame in Holland, some of our most successful exhibitors simply made a round of the farms and picked up their unbeatable pullets or cockerels for a few shillings. The same is true of Rhode Island Reds and Sussex to-day in England; a man who thoroughly understands what is wanted at the shows in these breeds to-day can often pick up a phenomenal winner at the farms. Exactly the same thing is true of Belgian horses and of several breeds of dogs.

It is not expected of show animals that they will breed true to

their individual qualities. In fact, in many instances the very standard of a show breed precludes breeding true. In some breeds of poultry, such as the Andalusian, the colour must be blue, and blues when bred together always only produce 50 per cent. of blues. There is even a breed of cattle, the French "Race bleue", the colour of which makes it impossible to breed more than 50 per cent. of calves of the right colour from registered parents, and not very long ago some English fanciers have followed this ridiculous example by trying to establish the "Blue Albion breed".

In some real show breeds, some special combination of qualities is desired that does not depend upon genotype at all. The best examples of this are the marked breeds of rabbits, such as the English and the Dutch. In those breeds a general sort of a pattern is determined by heredity, but the actual placing of each individual spot is determined by chance. In such breeds the production of a winning animal, after the correct sort of breeding stock is chosen, is wholly a matter of chance. In the long run those breeders will have the best chance of producing the winning Dutch-marked rabbit or Dutch-marked guinea-pig who produce hundreds and hundreds of youngsters. To a certain extent in such breeds individual excellence is no mark of quality as breeding stock; mismarked Dutch rabbits or English ones of good parentage are as likely to produce winning offspring as the winners themselves.

In some peculiar instances the chances of producing show winners are even better, if correctly-marked or correctly-coloured animals are not used for breeding at all. This is always so when the shows prefer heterozygotes. The Blue Andalusian fowl is a case in point. The mating of two blues together will give 25 per cent. black, 50 per cent. blue and 25 per cent. dirty-white chicks. Only the blues are eligible for show. The breeder of Andalusians who knows his business will always sell the blue birds he does not require for showing himself. For breeding he mates the blacks with the whites, for he knows that this mating will give him 100 per cent. blue chicks from which to select his winners.

English rabbits must have a certain medium quantity of coloured markings on a white background. Two such animals mated together will always give only 50 per cent. with the right amount of colour, from amongst which the breeder will have to

find his winners, 25 per cent. of very light ones and 25 per cent. of solid-coloured ones. The breeder who knows his business will always mate the light ones to the solid-coloured wasters, because he knows that these matings give him 100 per cent. of young with the desired amount of pigment, so that he has twice as many chances to produce a winning animal as the man who plods on mating correctly-marked rabbits together.

In dogs something like this exists in the Gordon setter. The fashion of the moment calls for a certain amount of tan on the feet, and this is only found in dogs carrying red as a recessive. The red puppies which are always born in this breed come in very useful, as they will, when mated with dogs with too dark a tan, give black-and-tan pups of the fashionable shade. In those countries where all-red Gordon setters are not eligible for registration, such red animals can only be used fraudulently.

In the Blue Albion cattle we have exactly the same thing. The only way to produce a blue calf with 100 per cent. surety is to mate black to white, for matings between two blues will always give as much chance to produce a black (or a white) calf as to give a blue one.

In some birds and animals the only reasonable way to produce show stock is to buy pure-bred breeding stock. This is especially true where the animals are monogamous or nearly so, as in pigeons or silver foxes. Most animals, however, are polygamous, so that one male is sufficient for a great many females. This means that a beginning breeder can save a very great amount of money by buying just one single male of the right kind and by breeding up his own strain from it. Of course, it is understood that this can only be done when we are dealing with animals where pedigree is of no account, or at least where no closed herd-book exists together with the regulation that only registered animals can compete at the shows. One of the reasons for establishing closed herd-books lies in this very point, that it forces new breeders to buy a number of pure-bred females at good prices.

Closed herd-books, however, are not common. In most real show stock, quality, that is beauty according to the fashion of the moment, is worth much more than pure breeding. This makes it possible for a beginning breeder who wants to economize, to make his start with just one good male. He will mate

this male with some females, and in selecting those females health and cheapness are worth much more than show quality. The best thing he can do is to buy females that are rejected for some reason connected with show judging, females with an unfashionable colour, females with a glaring fault, or animals of this kind. It is very hard to lay down definite rules, when speaking of breeding show stock in general, as things vary very much as between different animals. Where possible a beginning breeder should try to buy females that exhibit some recessive character, which excludes them from the showyard. I will give a few examples of this in different stock.

Let us say that somebody wants to commence breeding Lincoln sheep for show purposes. He buys a prize-winning ram and looks around for ewes. He can now either buy cross-bred ewes or Lincoln ewes of inferior quality, and build up his herd by the repeated use of his old ram or a good successor. If, however, he can buy black ewe lambs out of the flock of a well-known show breeder, this is the best purchase he can make, for if his ram is homozygous, this gives him a crop of excellent pure-bred lambs to go on with.

In those animals where it is customary to send females to stud animals, it is not necessary for a beginning show breeder to buy his own male at first. A breeder of dogs can make a start by buying one or two bitches, which must be of a good strain, but need not be perfect in themselves. He can then have those bitches served by the most fashionable stud of the period, and save a few of the female puppies for his own further breeding.

One of the surest ways to produce show winners is to in-breed to a fashionable sire. When a daughter is bred to her father, and a daughter of this mating is again bred to him, a breeder is reasonably sure of producing animals whose genetical make-up comes very close to that of the sire. This method is only feasible in those animals where males are kept for breeding for several seasons, especially in horses and dogs.

It often happens that a breeder, who has a considerable amount of capital invested in animals of a certain breed, wants to go in for a different breed which is becoming fashionable. Is it possible to change from one breed to the other by repeated cross-breeding?

Many recent examples exist in which a herd of animals is changed over from one breed to the other by repeated cross-

breeding, and it is really astonishing how quickly this process goes, if it is somewhat hastened by judicious selection. When at the beginning of the first world war a number of famous Belgian studs were imported into the southern counties of Holland, the whole horse population of Zeeland and Limburg was changed over into horses of the Belgian type in three or four generations. When a breed of horses suddenly becomes popular, as the Arab became popular in England some years ago, it is quite feasible to build up a stud of good Arab horses from almost any small herd of mares, when the services of a very good Arabian stallion can be had reasonably. One of the important things to remember in such cases is never to let oneself be tempted to use one of the good-looking home-bred males for breeding purposes, for such animals will be heterozygous for important genes during many generations. With females this does not matter, as long as they are bred to pure-bred and presumably homozygous males.

In some breeds of birds or animals a certain amount of variability exists even between the best show individuals. In those breeds strict selection of the best, most beautiful individuals for breeding will bring a breeder to the top. This means that it pays to breed a great number of individuals in every generation; the more extensively one breeds, the better is one's chance of producing something very good. The oft repeated saying that in breeding it is better to aim for quality than for quantity is certainly incorrect; the only way to produce quality from good foundation stock is to breed a large quantity of young stock, from which to choose the best.

In some breeds the stock is relatively very homozygous, and there is really very little to choose between the best animals at the top of the breed. By repeated selection and considerable inbreeding the good animals or birds have become closely related and genetically practically identical. In such instances the only real progress attainable is possible by means of cross-breeding.

When the ideal in any quality in a breed is hard to attain, and when we see that in a different breed animals excel in this particular point, the advantage of cross-breeding is obvious. A few examples will illustrate my point.

The breeders of Magpie pigeons were aiming at a bird with a thin, long, angular neck, and for some time there was really very little to choose between the prizewinners in this respect. The

Magpie was crossed with the French Bagadette, a bird with a very long neck, but otherwise very different from the ideal Magpie. The hybrids were mated back to Magpies, choosing those with long thin necks, and from a succeeding back-cross to Magpie was produced one bird that swept everything before it at the pigeon shows.

The case of the Dutch Pouter is very similar. Mr. Spruyt, in order to enlarge the feathered boot in this breed, bred some hybrids with Dutch Booted Tumblers. From those hybrids, mated back to his Pouters, he produced some prize-winning birds that were able successfully to compete with the finest birds in the breed. The same breeder, in order to enlarge the size of his breed, crossed some Pouters with Runts. The hybrids were massive, but had hardly any foot-feathering. Nevertheless, from these birds, mated back to good Pouters, he again produced a few birds that were remarkably successful in the show cages.

When in the modern Collie the judges began to award the best prizes to dogs with long, narrow skulls, somebody hit upon the scheme of crossing the breed with the Russian Borzoi. The hybrids were probably mated back to Collies repeatedly, and the modern show Collies of the present day all derive their present type from this cross.

The breeders of dogs, especially in England, often make use of cross-breeding to change the type of their dogs. The advantage of a cross lies in the great variability that results from it, and makes it possible to change the breed by continued selection.

The fact that the requirements of the show standards are dictated wholly by fashion is best illustrated by the fashion in dogs. In many breeds this fashion changes remarkably rapidly, and often a noted show winner is as much out of date as a lady's hat of the same period.

For a geneticist who makes a practice of following the shows of all sorts of animals and birds, the way in which show breeds change is of very great interest. The process seems to be somewhat as follows. At one moment a certain type of head is very much in vogue. To improve upon this somebody makes a cross, and as a result he produces in two or three generations animals that beat all others. As a result of the cross, however, those prizewinning animals have hair of a somewhat different type. As the judges see this sort of hair in the prize-winning animals, it is gradually looked upon, first as not too big a fault, next as

the usual thing, and lastly as the desirable quality of hair in the breed. So the process goes on, until the breed is changed completely. A few examples of breeds that have changed completely in this way are the Collie and the Airedale terrier, the Simmentaler breed of cattle, the Fantail pigeon, the small type of Poland China pigs.

In the preceding examples the reason for cross-breeding was the fact that a desirable quality was found in some different breed. This, however, is not the only way in which cross-breeding can be useful to the show breeder. Very often it is possible to use a cross in order to improve some quality that is not very highly developed in the breed used for crossing. When we are breeding some bird or animal in which colossal size is the main point, after some generations of selection most animals in the breed will have the combination of inherited factors that makes for the largest size in the breed. This does not mean that all the possible genes helping to make the animals larger are present in the breed, or that in the make-up of the best animals there may not be a few factors counteracting growth. In such circumstances it is quite possible that useful factors may be present in animals of different breeds, which might not even be very large in themselves.

It is a well-known fact that almost always the variability obtained in the second generation of a cross is transgressive, which means that in all sorts of respects more excessive extremes are reached in that generation than in any of the crossed breeds or species.

The plant breeders know that the best way to produce plants that are extremely frost resistant is to hybridize two varieties that are both rather highly resistant, to raise a large second generation and select a new extremely resistant type from among this generation.

The same is true in animals. It is not very probable that even in Flemish Giant rabbits or in Irish Wolfhounds has the ultimate size been reached that is possible in breeding rabbits or dogs. The same is true when we give our attention to such miniatures as the Yorkshire terrier or the Rosecomb Bantam. In Lops (rabbits), the extreme ear-length obtainable has been vacillating about the same maximum for the last ten years and it is highly improbable that straight selection could greatly improve it. It is, however, almost certain that the breeder who

takes the trouble to cross-breed the different breeds mentioned with not too closely related breeds, and to raise a large number of descendants from such hybrids among themselves, will actually produce rabbits that are larger than our present giants, or smaller than our present dwarfs.

When in one breed one reaches the extreme to which any character can be brought by selection, this does not mean that this is the ultimate extreme. It is very probable that in different breeds there exist inherited peculiarities that, when combined with the inherited make-up of the breed we want to improve, will make it possible to continue with the selection. This is the opportunity of the show breeder who has intelligence enough to use the method. Most breeders are discouraged when a cross of their breed with some other one produces unsatisfactory results. This is only what we must expect; if a cross helps us, the benefits of the cross cannot be expected to be visible unless we breed one or two generations from the hybrids.

In this chapter on breeding for the shows, something must be said about new breeds. Especially in the smaller animals and birds, new breeds are continually turning up at the shows. There are two sources of new breeds: they may be imported, or they may be made.

Importing a novel breed in itself is not very difficult, but from experience I know that it is well to observe certain rules in importing novel show breeds. When we can choose between several breeds to import into our own country, the breed to choose is the one that is the least like any of the breeds already existing at home. A breed of rabbits or dogs or pigs that look very much like one of the breeds at home has not as good a chance of "taking" as a breed that is a novelty in every respect. When the Samoyede was first imported into England, the importers did not take animals of all the different colours existing in the country of origin, but they imported striking-looking all-white dogs, for the very good reason that no fairly large breed of all-white dogs existed in England at the time, so that this group of imported dogs stood by itself as a striking novelty.

The Arabian Greyhounds have been imported from Africa. The first time when these dogs were imported into France and Holland, short-haired dogs were chosen and called "Sloughi". They never made very much headway, and the probable reason was that the general public did not easily distinguish them from

the European greyhound. Later on, long-haired individuals of a similar sub-breed were imported under the name "Saluki". Those animals looked strikingly different, and were much more of a commercial success for their importers.

It is a good rule, when importing a breed of sheep or dogs or pigeons, to select for importation striking-looking specimens such as are not even common in their own country. This makes it less easy for subsequent importations to compete with the first imported stock.

We must realize that the value of show stock is never determined by economic usefulness, but always by a relation between demand and supply and by wholly arbitrary standards of beauty. The standard of beauty of a newly-imported breed is wholly determined by the quality of the first few animals imported; once a breed has been established in a new country this standard of beauty is relatively fixed, so that animals that are imported later will be judged according to this standard. This means that very often a breed of animals will be different in one country from what it is in some other country, and it also explains why the show standards differ from one country to another.

Whereas the fancy of breeding animals and birds for shows is developed most highly in England, Holland, Belgium and Germany, in England we find the art of making money from breeding for the shows very much more highly developed than in the other three countries. This shows itself most strikingly when we observe the position of imported breeds in England. A typical English show breed like the English Game is bred in dozens of colours, but a typically imported show breed like the Flemish Giant rabbit, which in Holland, Germany and Belgium is shown in eight or nine colours, is known at the English shows only in the colour of the first few animals imported there.

While the show fanciers on the Continent often make the mistake of accepting the prevalent English show standard for breeds imported from England, in most instances the English fanciers soon after importing a foreign breed establish a standard of their own devising, somewhat different from the Continental one, and this effectively cuts off foreign competition, as it is intended to do. The most notable examples of this can be found in the pigeon fancy and the dog fancy.

There is always money in a new breed, quite apart from the

actual merit of the animals. The fact that only a few animals exist, so that the demand, once created, is greater than the supply, makes it profitable to breed a new bird or a new show animal. Some people who realize this make a point of always breeding the newest breeds for some time, always dropping a breed that happens to become common and taking up a newer one. This is not everybody's work—one needs very pronounced qualities in order to be able to create a "boom".

It sometimes pays to make a special breed of animal—one that combines the desirable qualities of two other breeds, but in so far as the making of show breeds is concerned, it is always best to make only such novel breeds as can be easily compared with others already existing. When we make a new colour-variety of an existing breed, this novel breed is accepted more easily if it can be seen that in the most important other respects the animals are of excellent quality. A novel colour-variety of the Leghorn can at least be judged as a Leghorn, or a blue-pointed Siamese cat will be accepted by the fancy if it is a Siamese of good quality.

Such novel sub-breeds are more often found by accident than not. In every breed recessive novelties are apt to crop up, and a breeder who is sufficiently conversant with genetics can easily make a new breed with the aid of even only one strikingly different individual. The example of the short-legged Ancon sheep is well known. I have already spoken of the blue-pointed Siamese cat. The Golden Labrador is another example. Some years ago I found one white pullet in a batch of common brown Barnevelders, and in a few seasons, by means of this one bird, I produced the recessive white Barnevelder, a breed that is equal in every respect to the ordinary laced Barnevelder, including egg colour, and different from it only in being wholly white. In the special chapter I show how a new breed can also be made out of an existing one by adding one gene by means of repeated back-crosses.

In a few cases new breeds resulting either from "sports" or from cross-breeding have been either erroneously or deliberately passed off as importations. The instances in which strikingly handsome animals or birds of very uncertain origin have been found in hybrid groups and imported as foreign "breeds" are not very different. The Sumatra fowl is one example that readily comes to mind. It is very certain that it would pay a

poultry fancier to visit the bazaars and markets in Java and the Malay Peninsula to look for strikingly beautiful new "breeds" of poultry, especially in regions where many species-hybrids are produced.

I have already spoken of the great importance for breeders of show animals to study the individual idiosyncrasies of show judges, so that they will know under which judge particular animals have the best chance of winning prizes.

Of very great importance, especially in some animals, is a thorough knowledge of the non-inherited factors that go to the making of a first-class show animal in prime condition. In some dogs and sheep one must know just where to trim off some more hair, to make the animal appear bulky in one spot, slender in the other, according to the fashion of the moment. In cattle and swine one must know just how far to fatten the animal for the shows, and just how long in advance to start doing it. Legion are the small tricks employed to change the appearance of the animals prepared for show, and it is necessary to know just how much trimming and faking is permitted. No general rules could be given. What is perfectly legitimate in the Cocker Spaniel, trimming away some hair to make the ears appear longer and the head higher, would be considered a crime, debarring the fancier caught in it, if it were done in poultry. On the other hand, the cutting off some black feathers in the white topknot of a Polish fowl is permissible, but pulling out or cutting away a small white blaze on the chest of a miniature Pincher would be an offence severely punished. Massaging away surplus flesh in spots where too much shows in show bulls is quite permissible, but a subcutaneous injection of turpentine to raise a depression on the surface of the same animal would not be allowed.

Sometimes the show-yard ideals happen to be so ridiculous that bringing an animal in first-class show condition ruins it. This is especially true in swine and bulls, where the judges cannot see their good points unless they are shown rolling fat. Keeping a bull in show condition for some time often renders it sterile, but in some instances the enhanced value its sons will attain when the father becomes a champion will offset the drawback.

It is a popular fallacy to believe that real enthusiasm for a breed is a prime necessity for a successful breeder. If success is to be measured by monetary gain, this is certainly untrue; those

people make most money out of the show business who are good advertisers and good business-men or business-women, level-headed enough to drop the breed they have been boosting, in favour of another one that has just become more popular.

To be a successful breeder of show stock one should first pick some breed that promises to be popular and adapted to one's circumstances. For some obscure reason that I have never been able to grasp, different classes of animals find their devotees under different categories of men; it can even be said that men are attracted to some animals, and women to others. Why should it be that the breeding of show cats is almost wholly in the hands of ladies, whereas there are as many men as women among dog fanciers and rabbit fanciers, while pigeons are essentially a men's hobby?

Next, the beginning breeder must buy some good breeding stock, and he or she must start at once to "boost" that breed. He must study the shows, and exhibit carefully-prepared animals just where the chances are best that they will give a good account of themselves. Most important of all, the breeder must thoroughly get rid of any notions he may have that there is a logical reason for any point admired in the breed. The legs in one particular breed are not long (the longer the better), because this gives the animal great speed, but simply because the judges to-day like to see them long. Ten years from now the judges of that day may prefer to see them moderately long or even short.

If there is any correlation between show points and economically or physiologically useful qualities, this should not concern the show breeder other than as a striking point in his efforts to boost the breed; he should not act upon his belief when fashion goes the other way. Showing has nothing to do with utility at all, it is simply a competitive game, and the way the fancy goes should never be taken too seriously by any of the insiders.

The breeding of show animals, especially of the smaller kinds, is a hobby that brings quite a lot of interest in a great many otherwise humdrum lives—and this is the best that can be said for it. Further, a few people make money by it and that is the next best point.

NOTES

This chapter, packed with inside information and worldly wisdom, must surely be unique. All agricultural students should be advised to read it, and most agricultural journalists be compelled to swallow it!

Chapter Thirty-Seven

The Influence of the Show-ring

When a breed of animals or birds becomes of some importance, it will soon make its appearance at the shows; and showing the breed is apt to have its influence upon the variety in different ways.

This influence begins very early when a novel breed is imported into some other country, for only very rarely is the group that is imported a random sample of the breed as it exists in its own country. Generally the group is selected for importation—a group that is much more homogeneous than the whole breed, as the fancy of the importers made them choose animals of a certain colour or a certain type.

Exactly the same thing is true when a breed of animals which has been bred for a long time in a certain country is first shown. The Keeshond in Holland originally was bred in two colours, wolf-grey and white; but when the breed was accepted as a show breed, for some obscure reason the whites got excluded. This fact made the breeders discriminate against the whites, so that gradually the majority of animals in this breed of dogs have become grey instead of white. The whites however are still very popular in the U.S.A. but not at the shows.

This discrimination at the shows in regard to one definite type, or of one definite colour, produces its influence upon the breed in many ways. The first effect is an appearance of uniformity, which is not necessarily related to a real uniformity, but which may be the cause of a subsequent reduction of variability. A more important influence upon the breed lies in the fact that it makes conformity to the chosen type more important than many other qualities of really much greater value.

Herein lies a grave danger of the influence of the shows.

There are in every breed a number of qualities that cannot be judged at the shows but that are of the greatest importance for the use that can be made of the animals. The ability of a cow to produce milk cheaply, the temperament and sense of smell in a sheep-dog are of much greater importance really than the length of the tail and shape of the back in the cow, or the way in which the dog carries its tail, but as these latter qualities can be judged at the show they are apt to obtain a selection-value that is out of all proportion to the value of those characters in the animals. Very often animals that are not really good specimens of their breed may have a fictitious value as breeders attached to them as a consequence of their being highly recommended at the shows. A nervous or a gun-shy hunting-dog may become celebrated as a show dog, and as a result may be used for breeding extensively; a bull that produces as many poor heifers as good ones may be so attractive that he is used for stud purposes instead of being scrapped, because he gets a championship at a show.

The exhibition of animals at shows is good business from the point of view of the breeder, who makes his living selling breeding stock, and the shows have formerly done great service in getting the farmers interested in breeding good stock; but the question may well be asked whether the show system is not responsible for much more harm than good from an economic standpoint.

Different causes have contributed to the idea that the qualities we judge at the shows are correlated to economically important characters in the breed, and this idea has justified judging the animals according to exterior. Breeds differ from breeds, and families differ from families in economic qualities as well as in small show points, and it is easy to mistake this connexion between the points of a breed and its intrinsic qualities for a causal relation. A certain breed of milk-cattle may be characterized by a low-set tail, and an excellent family of raccoon hounds may have exceptionally long ears. This does not mean that there is any causal relation between set of the tail and milk production, or between ear-length and hunting ability; it simply means that the breed happens to have a set of genes that is responsible for ear-length or shape of the tail, and at the same time a set of genes that makes the animals excellent from a user's standpoint.

It is evident, however, that once we introduce those fancy points into the standard of perfection of the breed, the breeders in selecting breeding animals will give more attention to those easily-judged qualities than to the more important qualities that do not happen to be of such a nature that we can evaluate them at the shows.

In some instances a certain interdependence between qualities of economic value and easily-judged exterior points does exist, namely in those instances where the effects of high production can be seen in the animal. A heavy season of milk production gives the cow a set of easily-recognized qualities; a long laying season will have its visible effects on the body-shape of a hen. This may result in the possibility of selecting a good producer of a breed one knows at a sale, and it is not surprising that judges may start looking for these qualities in the animals presented to them.

Whenever anybody has taken the trouble, however, to study the correlation between show points and economic value, this correlation has always been shown to be insignificant.

A great deal of harm has resulted from taking such show points into a standard of perfection to be used in selecting and rejecting animals for a stud-book. This has resulted in setting up false standards of usefulness to breed up to, and sometimes it is very difficult to get back to a reasonable basis for selection.

Boutflour has summed up the situation in the following way. Either there *is* a correspondence between show points and utility, or there *is not*. If there is, it is clearly unnecessary to select for show points, for they will automatically follow if we select for real value. If there is no real causal connexion between the two, it is evident that selecting for show points, when aiming at improvement of economically-important points, is leading us astray.

In the production of some kinds of animals, namely, those that are bred for no other purpose but to win prizes at the shows, the shows fulfil a real need. As the fashions in show animals change, it is continually necessary to keep on selecting and cross-breeding to keep in the swing, and very many people obtain great satisfaction from doing this sort of thing and producing animals that will win at the shows over the animals of their competitor. There is no harm at all in this game, which

provides a great many people with an interest in life and incidentally enables a few breeders to earn money by following the fashions and selling prize-winning stock.

In the production of economically-useful animals, however, such as cattle, swine, egg-laying breeds of poultry, and horses, the show-ring is more of a menace than an aid to breeding.

NOTES

The last sentence of this chapter sums up Hagedoorn's considered opinion on the place of the show-ring and showing in the economic improvement of livestock. He says what very many must feel but are diffident to express because of the enormous prestige that successful showing still enjoys. Hagedoorn had the courage to speak his mind, and I am convinced that what he said is entirely justified.

Chapter Thirty-Eight

Scientific Investigations and Animal Breeding

Although a considerable amount of scientific research has been done on domestic animals, most of this work has been concerned with the utilization of animals. Much of what we know about the feeding of cattle and swine is the result of painstaking experiments in different fields. In most of these investigations, however, the constitution of the animals concerned has been taken for granted, and very little serious work has been done on the improvement of the animals themselves.

As the animal breeders are concerned with combinations of genes, it seems evident that investigations that have as their object a knowledge of the different inherited factors should be of the utmost importance. We geneticists in our purely scientific work are always striving to analyse the genetic factors that differentiate our experimental animals, and we cannot be surprised that the first geneticists who concerned themselves with animal breeding had the impression that it would be useful, or even absolutely necessary, to analyse all the genes in our domestic animals, in order to build up ideally useful breeds from those building-stones. This idea has been proved erroneous. It was based upon a misconception of the number of genes concerned in the differences between our animals, and of the action and interaction of genes in development; in fact, it was based upon the Weismannian conception of genes as determinants, each for a special unit character, and of the organism as a mosaic of separate, separable characters.

In other chapters I have treated of this part of the subject and have given a warning against attempts to foist upon the public quasi-genetic schemes with four or five Mendelian factors. Yet

I would not give the impression that factor-analysis in domestic animals is valueless from a practical standpoint. It is very important that pure science shall go on, unhampered by practical considerations, as applied science is always a by-product of pure science, and nobody can ever tell where the practical applications will come from. One direct practical result of factor-analysis in poultry, for instance, has been the production of the new auto-sexing breeds of poultry.

When it becomes possible to substitute Canutian Government regulations for the inter-play of supply and demand, and to divert a fraction of the money now spent in attempts to regulate animal breeding to the necessary investigations in the interest of the breeding industry, it will be necessary for geneticists to state just what kind of investigations are of primary importance.

From a knowledge of plant and animal breeding as well as genetics, I emphatically state that investigations with factor-analysis as their object are not of prime importance.

Of very great urgent present importance are investigations destined to criticize methods of selection. If we could find some money for solidifying the scientific foundations of animal breeding, we should take the lessons of plant breeding to heart. It is very clear that in plant breeding the greatest advance in the last twenty-five years came from novel and better methods of selection and the making of novel combinations of genes, generally unaccompanied by factor-analysis.

In animal breeding there are three fundamentally different methods of obtaining a good fit between the nature of a breed and the direct environment in which it must be put to use.

(1) First, there is the method of selecting the best breed from among the numerous breeds available, and this includes trying breeds imported from other countries. Up to the present the main progress in animal breeding has been due to this method, mostly by a rough and ready method of often wasteful trial and error. Although this trying out of different breeds and local sub-breeds is of extreme importance, it is not really a matter of applied genetics, and no special institute of animal breeding should be necessary for it if the zoötechnicians know their business.

(2) The second method is that of producing new breeds by a deliberate process of re-combining material present in

separate breeds and species. This is of great importance in plant breeding, and should be of equal value for animal breeding. Even in poultry it cannot be said that any considerable work has been done along those lines; the economically useful breeds have originated mostly either as show-breeds or as local land-races, without any deliberate method. The two most important breeds of domestic birds, the Khaki Campbell duck and the White Leghorn fowl, are striking examples of this.

It should be recognized that there is no reason for making new breeds until we know that the existing ones have definite faults that could not be bred out. As long as in the existing breeds a number of individuals are exceedingly valuable there would be no object in trying to construct new breeds. In poultry, however, where making a new breed is something which we know can be done for a few hundred pounds, and where no ideally good breed exists, the deliberate construction of a new breed combining the good points of some of the existing ones could very well be undertaken by an Institute of Applied Genetics, with expectation of complete success.

(3) The third method of improving domestic animals is selection within the breeds. This is the most important subject of all. The object of selection is mainly to produce uniformity for those qualities that are now present in the very best animals.

Animal breeds are mostly exceedingly variable. Some animals excel in one respect, others in different ones. In many breeds, aberrant individuals are very often produced, very few breeding animals having such a make-up that all their offspring are valuable from a user's point of view. Even a very superficial study of methods of selection in use shows that in this respect animal breeding is lagging considerably behind plant breeding. Methods that were abandoned in plant breeding because a thorough investigation of their practical value showed them to be absolutely worthless are still in use in animal breeding.

This, to my mind, is an exceedingly promising field of study for an institute of animal breeding. The methods of selection in use can be roughly divided into three groups:

(*a*) The first method employed is that which we could call the method of selection according to individual merit. This is the most obvious method, which is in use even where primitive men keep animals, the method of saving for breeding the very best individuals.

When geneticists started to investigate the results of these methods in plants and animals, the result was astonishingly disappointing. Ten generations of selection of the heaviest layers, mated with the sons of the very best layers, was shown by Raymond Pearl at Maine Experiment Station to have produced no effect whatever. We could show that even fifty generations of strict selection in wheat did not result in changing the characters of the ears in any way.

Geneticists know pretty well why this method fails in so many instances. Individual value is the result both of inherited make-up and of a favourable combination of environmental circumstances, and the effects of these latter are not transmitted. A good animal may be heterozygous for many of the genes that make it excellent, so that only part of its offspring inherit those genes. It is extremely important, however, that such methods should be the object of experimentation. It is not sufficient that we know that selection for individual merit is ineffective in wheat and mice and poultry; it is necessary that we should know how efficient the method is in swine, in dairy cattle, in sheep, in horses.

(*b*) The second method of selection is that in which the bases of selection are qualities that are not sought for because they are of great value themselves, but because they are thought to be correlated with the qualities we value most. Breeders look for a well-shaped udder in heifers because they believe this shape is correlated with milk yield; they prefer swine with thick tails, because they are convinced that such swine are using the food consumed more economically than thin-tailed hogs. I have given many examples in the chapter on Correlation, and I have discussed the subject at some length. Here we are concerned with the possibility of studying the basis of such methods experimentally.

Very few geneticists have taken the trouble to investigate just how a belief in some of those correlations originated, but when we have started to inquire into this subject we have always been shocked to find that we are almost invariably dealing with pure superstition. In a very few instances the belief in a correlation is due to a faulty method of thinking, or to unwarranted generalizations, or to the observation of accidental association of two qualities in one breed.

In plants the methods of selection based upon supposedly

correlative qualities, instead of upon the actual qualities sought, have gone out of fashion, and are now only of some historical interest. These methods disappeared, partly because investigation showed that the correlations most firmly believed in did not in fact exist, and partly because even where correlations did exist, safer and less roundabout methods of selection came into general use.

In animal breeding, exceedingly little has been done to investigate the value of even those instances in which a belief in correlations is most firmly held. I have no respect whatever for firm beliefs in such matters, for I have seen that in the few instances where those beliefs were put to the test of an investigation, they were found to be wholly unfounded. The rankest superstitions tend to be most firmly believed. When breeders believe that a straight back and heavy feet are correlated with robust constitution, we tend to think that they do this because of experience. When, however, we find that these beliefs are based on no solid grounds, we begin to see that it is time for somebody to take the trouble to put these opinions to the test of experimental investigation.

This is not inherently difficult, only such investigations cost time and money. When in a given year, several years ago, a hundred heifers were lauded in the agricultural journals and were registered after judging because they had excellent constitution, as shown by the straightness of their backs and the solidity of their legs, it should have been possible to inquire into the whereabouts of those cows, to find how many of them were still being milked as eight-year-olds, how many had been scrapped, and why. It should be possible to do the same thing for a hundred heifers that were denied registration for having weak backs or insufficiently solid feet. In this way we could find out whether there is any truth in the belief that straight back and solid legs are signs of robust constitution.

In horses the belief that robust constitution can be judged in the young animals by looking at certain bodily proportions could easily be put to experimental test.

In swine it would be very useful to see whether there is any truth in the universal belief that thinness of legs is correlated with leg-weakness, and whether a wrinkled forehead is correlated with poor butchering-quality. Such investigations would cost time and money, but this money would be very well spent.

In dairy cattle statistical investigations started by Mr. Buursma and later extended and corroborated by Mr. van Oers in Holland have shown that the correlation between excellence in such show features as points for back or legs or loins in bulls and those same qualities in their daughters is negligibly small.

The amount of energy and money involved in animal breeding based upon correlative characters is prodigious. This whole edifice is erected upon a foundation of untried solidity. Speaking from the experience derived from a knowledge of plant breeding I am very much afraid the foundation is not only untried but thoroughly unsound.

This should be the very first object studied by an institute of applied genetics that would have the importance of sound methods in animal breeding at heart, because of its great value for agriculture.

(*c*) The third method of selection in animal breeding is the method treated in the chapter on progeny-tests. This method is founded upon a healthy distrust of theoretical considerations in the matter of selection.

There is no getting round the truth that that animal which weighs most is the heaviest animal. In the same way it is an obvious truth that that animal which gets nothing but valuable daughters is worth more as a breeder than his brother who gets good daughters, mediocre ones and bad ones, everything else being comparable.

Selection according to progeny-tests is a method of working that deliberately scorns to make use of any of the proposed short-cuts, and acts upon the sound empirical principle that the proof of the pudding is in the eating. It is the only method of selection that has been proved to be of any value in plant breeding.

Experimental investigations in this field are necessary to test the value of different fringes, tacked on to this method to make it appear either more imposing or more acceptable to the men used to old-fashioned methods of working. Half a dozen more or less complicated methods of producing bull-indexes have been invented, and most of these can be investigated statistically or even experimentally.

As far as these indexes give a picture of the male's breeding value as dependent upon theoretical considerations, an element of speculation enters. A plain statement giving the number of

offspring examined, and their quality, suffices to provide the breeder with a good working knowledge of the breeding value of a male, provided the group of descendants is representative and in no way selected.

Very often the examination of an animal's breeding value is made complicated. Instead of a mere statement of the real economic quality of the descendants, and nothing else, the examination also goes into external characters of supposed value because they are believed to be correlated with real economic value. Although it seems evident that this complication lessens the value of a simple sire index, it is certainly worth while to study such instances exhaustively, to find out just in how far they give a wrong picture of a sire's value.

In the breeding of poultry and ducks it has been found that the method of selection consisting of choosing the best group of offspring from several such groups, each by one sire, basing the choice on real economic value of the daughters only, works very well.

It should be tried in other livestock. If it were found that we could base selection in swine exclusively on the value of groups of offspring produced by different fathers, without looking at supposedly important external points at all, either in parents or offspring, this system of selection would automatically result in profitable strains.

In our present methods of animal breeding, too much depends upon plausible-sounding theories to let those theories go unchallenged. It is clearly the task of those in authority in such matters to give geneticists the opportunity to conduct these fundamental investigations.

[NOTE.—Five diagrams, Figs. 38–42, are appended on pp. 354–359, taken from *The Relative Value of the Processes causing Evolution.* These are related to subjects discussed in this chapter.]

NOTES

In this chapter, I rather feel that Hagedoorn, like practically every other geneticist who has concerned himself with the breeding of farm animals, tends to confuse methods with aims.

A great deal of the justifiable criticism at present being levelled against our Breed Societies and pedigree breeders is, essentially, a criticism of their wrong

aims *in selection. Were the* methods *of selection as ineffective as is so frequently suggested, then these wrong aims would be of far less danger to the economic usefulness of our farm animals.*

When a Breed Society establishes long, dangerously pointed horns or a face covering of blinding wool as breed points in cattle or sheep, then it can be justly argued that the aims *of such Breed Societies must be wrong if the breeding of farm animals is to retain any utilitarian and economic purpose.*

If Breed Societies could be persuaded to drop such fancy and sometimes frankly undesirable points for which to breed, and concentrate their breeding efforts on the economical production of that particular product for which any breed of livestock is commercially kept, then there would be far less justification for the criticism of Breed Societies.

For, as regards methods, *there is really no such great gulf between the methods used by every successful pedigree breeder and those being most strongly pressed at the present time by geneticists and other scientists interested in livestock breeding. Every breeder of pedigree livestock practises the Sire Performance Test in some measure, in that among his male stock, be they bulls, rams or boars, he will castrate those which in the course of their development do not come up to the standards of his herd. The real trouble is that, because of unrealistic aims in breeding, a male imperfect in some unessential breed point, say an unfashionable colour, is quite as likely to be castrated as one which grows slowly and makes an uneconomic use of its food.*

Similarly, successful pedigree breeders make use of a Progeny Test in that they bring every stock sire to judgment on the value of his get. The difficulty here is that a sire which leaves a very few outstanding individuals may be preferred to one that leaves more uniform and commercially useful stock. That is because, as Hagedoorn so frequently emphasizes, an outstanding individual is, from the show-yard point of view, of greater value than the most level lot of calves or lambs.

In any event it seems a trifle illogical to accuse pedigree breeders of doing damage to the commercial value of breeds by selecting for fancy points while arguing, at the same time, that the methods of selection used by such breeders are relatively ineffective. Were the method *of selection ineffective, then false* aims *in selection would obviously be of less serious moment.*

The newer outlook on the breeding of farm animals might more properly be called quantitative rather than scientific since the main innovation suggested is addition of measurement to observation. Mensuration is not necessarly more accurate than trained observation, and figures, in themselves, may not be so very scientific after all. So far, the most valuable contribution of the geneticist has been to concentrate attention on characters of economic importance for which to breed. There has been an improvement in aims, but the improvement in methods, so far, is rather less evident. The over-concentration of effort in measuring liveweight gains cannot be termed an unqualified improvement. At least in one meat animal—the pig—it has been shown that an animal, although excellent in respect to liveweight gain and economy of food conversion,

may be woefully deficient in the very product for which it is bred, namely meat. It has also been shown that the grading system devised by scientists and applied to bacon pigs may result in up to 40 per cent. of the pigs of the highest grade (and therefore presumed to be of the highest quality) being entirely unsuited to produce the product—namely bacon—for which they have been specially graded.

Again, in respect of progeny-testing, the first essential of a scientifically conducted progeny test is that the sample of progeny tested be a random *sample. In the systems of pig progeny-testing, both in this country and in Denmark, that essential is still being ignored, although Hagedoorn long ago drew attention to its omission.*

Geneticists, many of them lacking the detailed knowledge of the methods of the pedigree breeder which Hagedoorn possessed, are highly critical—and in certain instances, rightly critical—of those methods. It might, however, be a very good thing were such geneticists to realize rather more clearly than they are inclined to do that criticism, like charity, should begin at home.

Chapter Thirty-Nine

Breeding of Special Groups of Animals—I

Introduction. While it is true that exactly the same laws of nature govern heredity in all animals, I know from my own experience as an animal breeder and as a consulting geneticist, that in the breeding of every group of domestic animals special difficulties are met. The breeding problems of the man breeding bantams for the shows are wholly different from those by which his colleague, breeding Leghorns for egg production, is confronted.

In many instances the breeder of one sort of animals can easily do what would be out of the question for economic reasons in the breeding of another group of animals.

On the whole, it is desirable that the breeders shall not just work blindly, following the lines of least resistance, the dictates of the fashions, or even the counsels of geneticists, but that they will try to understand what they are doing. It is even very desirable that they shall try to understand what other breeders, and what plant breeders are doing. From experience in co-operating with breeders, I know how often it is possible to adapt the methods of one breeder to the needs of a second one. For this reason the bulk of this book has been devoted to a general discussion of the principles underlying animal breeding, and of working methods.

At the same time, it seems desirable that some space should be given to a discussion of the very special problems that confront the breeders of each special group of domestic animals and birds. The following chapters are necessarily very uneven. For one thing, many very special problems have been used as examples in the body of the book, so that most problems of some groups of breeders have been rather fully discussed in many

chapters. In writing the following special chapters, I start from the assumption that the specialist, reading the chapters that most closely concern him, has read the book, and very often I will refer him to one or the other of the general chapters.

In the following two chapters I have made no attempt to be exhaustive, and where I have no first-hand knowledge of the problems discussed, I say so. Many more groups of domestic animals exist than the twenty-six groups that are given special sections. A few have been left out altogether. I know nothing whatever about the camels and about the breeding of llamas and alpacas, as no breeder of such animals has ever deemed it advisable to consult me. I have no doubt, however, that even the breeders of these animals will find plenty of suggestions in the book to enable them to decide whether their present methods of breeding need revision.

The Horse. The number of horses per owner is still smaller than the number of cows, and this fact makes some of the difficulties we meet in cattle, still greater in horses. It puts still more responsibility on the shoulders of the stud-book authorities, and at the same time it increases the danger that a breeder will make unwarranted generalizations. Real breeding experience must be lacking in most horse breeders; a breeder who has bred thirty foals counts among the experienced horse breeders, but it stands to reason that this experience is as nothing compared with that of a poultry breeder.

The shows have had an enormous influence upon horse breeding, and in many countries a system of licensing stallions, and of prohibiting the use of non-licensed stallions, has been founded upon a system of judging for show points.

This system of stallion-licences was well established before we knew the real causes of prepotency and breeding value, and it much needs revision. It is certain that good-looking stallions of hybrid origin are sometimes licensed, while pure-bred stallions that look less brilliant, but are probably better as sires of the next generation, are rejected. There is no excuse for a system that is based on the fallacy that an animal's individual qualities are inherited. If a system of licensing stallions is necessary, it should be based upon a progeny-test, so that only sires that have produced a group of offspring (to be judged from a random sample) of good quality, are definitely licensed. Such a system

could be combined with stud-book registration in such a way that only proven sires can be definitely registered, and only sons of registered fathers can be licensed for use.

Wriedt's excellent idea of deferring registration of stallions until they have produced a certain number of offspring from their own daughters would, if applied, have the effect of eradicating lethals and less fatal inherited faults.

With those breeds of horses in which the animals are actually used for economic purposes, sensible tests of merit should be substituted for judging for show points. In a draught-horse we require pulling-power and staying-power, in correct proportion to the value of food consumed, and not simply brute weight per individual.

It is possible to change over one breed of horses into a second one by a system of repeated grading, in a very few generations. Horse breeders should remember, however, that this is an automatic process that can only lead to the complete change of one breed to the other. If a complete change into the new breed is not desired, this work should not be undertaken, and another breed that really fulfils all our requirements should be introduced. Improving an existing breed by the introduction of a "dash of blood" from another breed is an enormously difficult undertaking, which is beyond the power of horse breeders operating with a few mares. On a certain day the herd-book of the light agricultural horse in a continental country was split up into two sections. At a national show it was found later that the grand champions of the two types were related. They were father and son!

In importing a breed for use, the great mistake of taking the individual value of an animal for an indication of its breeding value should be avoided at all costs. The first thing we must know is, whether pure-bred animals of the desired breed, when born and raised under our own conditions, grow up into the sort of horses we want. It would have been impossible to prophesy that pure-bred Arabs born and raised in Java would retain their usual size, whereas hunter foals born and raised in the same spot would grow up as ponies!

In certain circumstances, first-generation hybrids between two breeds are of excellent value. In such instances these hybrids must be produced anew from pure-bred parents, and the mistake of using such hybrids for breeding, because of their per-

sonal value must be avoided. I am thinking of such cases as the excellent hybrid hunters from Thoroughbred × Suffolk Punch crosses, and of the Arab × cow-pony, riding-pony or polo-pony.

Very peculiar problems are involved in the breeding of race-horses. Here it is often seen that individual merit does not necessarily go together with breeding value, and some of the famous sires have been mediocre race-horses. In this work the aim is not to produce groups of foals of high average value, but to produce one or two outstanding individuals.

One of the most promising breeding schemes in race-horses is the duplication of a famous speedy sire. This can be worked in the horse, because of the great age to which studs keep breeding. My idea would be to breed back a few daughters of such a male to their father, mate the mares so produced to the "grandfather", and continue as long as possible, or until success is attained. This is a system of breeding for speed, which has a sound genetical foundation, and the same thing cannot be said for the fanciful systems of "blending", in which some breeders seem to have faith.

I have devoted a separate chapter to mule breeding. Attention should be given to the fact that some mare mules are fertile. It might be extremely valuable to introduce some of the donkey genes into a breed of working horses, via such fertile mares, to try to improve the breed in regard to economic food consumption in relation to work done, and in regard to longevity and staying-power.

Mule Breeding. The horse and the ass have been hybridized from immemorial times. The mule has a combination of qualities that makes it more economical to use in special circumstances than either the horse or the donkey. It combines the donkey's longevity, sobriety, toughness and level-headedness *with the horse's size and superior speed.* For special work, as between rows of potatoes, or in hot weather, mules are superior to horses. The intelligence of the mule, which is almost equal to that of the donkey and vastly greater than that of the horse, is an advantage in certain instances, such as work in pack-trains and in ploughing, but a disadvantage where an automaton is required.

Mules are produced mostly from biggish mares and very large donkey stallions. The reverse cross, which is made where

donkeys are very plentiful and cheap, is mostly bred from pony stallions, and such animals are mostly lighter and smaller. The mating of a Belgian or Percheron stallion to large Andalusian jennets, however, produces typical mules just like the ordinary cross, as I have been able to observe personally. The difference between mules and hinnies is certainly not due to mysterious influences of the mother on the foal, as in some other instances of difference between reciprocal hybrids.

Mule breeding is especially indicated in places where biggish mares of doubtful value are plentiful. It is astonishing to see the enormous variety between the mares and the uniformity in the mule foals, at any of the larger markets where mule foals are bought and sold. The mares differ as much as horses can possibly differ; the mules look as if they had been turned out by machinery.

For some reason white and grey mules are very unpopular in some countries. White or grey mares should not be used for mule breeding. The actual mating of the mares to the jack is a problem in itself. Donkey stallions are slow breeders. In French mule breeding districts people believe that the donkey stallion should never be allowed to mate with donkey mares, if he is to be used for mule breeding. All sorts of tricks are resorted to to get the jack to serve a mare, from trying to make him jealous up to what is called "le lalandage" in France. Anyone who has ever witnessed the ridiculous spectacle of a circle of stable-men joining hands and singing their aphrodisiacal "la-la-la" chorus around the hesitating stallion will be convinced with me that artificial insemination, which will allow the donkey stallion to mate with his own jennets, will soon be appreciated by mule producers.

Superior jack stock is found in France (Poitou), in Andalusia and in the Pyrenees. The right combination of two breeds is the main thing. Mule breeding should be combined with horse breeding, as it allows of the second-rate mares being profitably employed for the production of mules. Where it is necessary to produce the jack stock locally (and this is a very paying breeding industry!) jacks should be selected according to the sort of mules they produce, and in no other way. It is very unsafe to rely upon their size or upon the thickness of their legs as marks of quality.

Mules, at least some of the mares, are occasionally fertile; many instances have been described. The foals produced from

the mating of such mares both with donkey and back to the horse, have been proved to be fertile again. It is probable that the very large, horse-like donkeys one sees in the south of France and the north of Spain have some horse "blood".

It would certainly be possible to utilize the fertile foals from fertile mare mules to start a breed of mules that would be fertile and would free the breeders from the continued species-cross. Whether it would pay to do this is another question; I am convinced that it would most certainly pay in such countries as South Africa where in certain regions horses do not stand the climate (or the local parasites) well. In such countries breeding back the occasional fertile mare mule to horses would give the starting-point for a local breed of horses that would be adapted to the adverse local conditions. This is work that should be undertaken by Governmental experiment stations.

A very peculiar fact is that in parts of Africa, where horses are bred in country heavily infested with leopards, on the open range, half a dozen mules added to the herd will effectively protect the younger foals, when the mares would be unable to cope with this great enemy. I have heard the same story from a professional hunter in Californian puma country, where horse foals are also a favourite prey of the big cats.

The Donkey. Donkeys are used for the same purposes as horses, chiefly in localities or circumstances where the peculiar qualities of the species outweigh the disadvantages. The ability of the donkey to thrive in desert and semi-arid conditions is not wholly due to inferior size, for even the large mules are more sober in their food requirements than horses of equal weight. The donkey is very much more intelligent and level-headed than the horse, and this is of some importance where pack-animals are required; a disadvantage is the donkey's disinclination to go fast, which is exasperating in certain work. This is purely a mental quality, for even smallish donkeys can travel at a surprising speed when the occasion arises. Some of the Egyptian breeds can be used at a satisfactory speed.

Some of the Mediterranean donkeys (Sicilian) are veritable dwarfs, and can be used very economically where slow and light transportation is required. The largest donkeys are found in Spain.

The chief economic importance of the donkey for agriculture

lies in mule breeding. This is treated of specially above. Through occasional fertile mare mules, horse genes can be introduced into the donkey, and it is very probable that in some of the largest, heaviest breeds of donkeys this has been the origin of their superior size.

Utilizing fertile mare mules in the production of a fertile breed of mixed origin is a possibility that offers great prospects to enterprising animal breeders, especially in countries where certain properties of the donkey, such as its surefootedness and disease-resistance, are of very great importance (Africa).

Cattle. Cattle-breeding problems have been discussed all through this book; in cattle we see more strikingly than in any other animal group the great influence of the shows on animals that are really only bred and kept for economic profit.

If we include the yak and the different zebus, the group of domestic cattle is extremely varied, and breeds of cattle are adapted to the most diverse circumstances.

Systems of selection are in vogue, even to-day, that are clearly based upon erroneous principles. It is high time for it to be generally understood that only one quality is really to be sought for in cattle, namely, adaptation to systems of agriculture to produce the maximum of economic profit to the agriculturists who own and exploit them.

Fictitious value of certain animals, dependent upon show successes, may for a relatively few breeders bring along monetary gain, and when as here the few men who make their living from the sale of beautiful breeding stock are heard, while the majority of users who want good animals do not become vocal, there may come about a state of things that is economically very undesirable.

As cattle are highly polygamous, and can be made much more so by means of artificial insemination, the breeding value of males is much more important in selection than that of individual females. The most logical system of selection in milk cattle is that in which the breeding value of some bulls is recognized by testing the quality of their daughters, whereas the individual quality of the cows should be registered to make the recognition of good fathers easier. Selection based upon supposedly correlated characters is not only in itself without

value, but it may become harmful when it brings about a state of things in which too few excellent fathers are recognized.

Of the many bull-indexes proposed, I prefer the average quality of a random group of heifers, daughters of the bull, as being the safest guide to what we want a bull-index for: the probable quality of the daughters he will produce in future from the kind of cows on hand.

In countries where cattle breeding is controlled, the danger exists that herd-book or show standards are applied in judging male breeding stock, and that, instead of trying to breed cattle adapted to different economic circumstances, users are almost forced to breed the sort of cattle the judges approve.

By means of progeny-tests of bulls and artificial insemination, it would be perfectly feasible to prohibit the use of bulls from untested fathers, or from fathers that had been proved of doubtful value. In making such regulations however, every step should be taken to ensure that economic usefulness and not show-quality is taken as the basis for the progeny-tests.

The authorities should have more respect for breeds of doubtful beauty but excellent fitness to unfavourable conditions. We want cattle that the farmers find profitable, not necessarily cattle that produce a very great quantity of milk individually. Economic food consumption, the ability to utilize the locally available food economically, should be regarded as essential.

Bull-testing based only upon the quantity and quality of milk produced by a bull's daughters might lead us just as far astray as selecting for show characters. When we want economic production of sugar or milk, we are more likely to get it if we select for sugar per acre or milk per acre than if we select for sugar per beet or milk per cow. The advocates of modern systems of bull-testing are underrating this danger, probably because (as Goodale and Prentice at Mount Hope) they only know cattle in conditions of agriculture where very large cows can be profitably kept, even if the cost of food is high.

In selection it is always dangerous to think that we can neglect a possible source of danger, because we can deal with it later on. This was the great fault of the system of selection for apparent "constitution" in milk cattle, and when we once recognize such faults we should always avoid them.

The importance of raising first-generation hybrids for direct use, especially for beef, has never been sufficiently investigated.

Experiments in cross-breeding to find the most profitable combinations of breeds or species (yak and zebus should be included) are beyond the scope of the work of individual breeders. Such experiments should be done by combinations of persons, either by firms interested in beef production (packers) or by Governments.

The quality of isolated non-selected local breeds, such as the Dutch Belted and the Gloucester, should be investigated, as some of these breeds are probably excellent for certain conditions when food consumption and milk production are both considered.

The study of real constitution, the ability to keep up heavy production for a very long time, should be taken up, notwithstanding the fact that up to the present selection for "constitution" has been mainly based upon error.

The Santa Gertrudis for Queensland. Being very interested in the birth of new breeds of sheep and cattle from crossbred origin, I have followed the history of the Santa Gertrudis breed for several decades.

To make a really new breed of cattle from crossbred stock is an enormous undertaking, when we are not content with having just another more or less pure-breeding group, that looks different, but when the aim is to make a breed that shall exactly fit local conditions of animal husbandry, local climate and grazing conditions, and that will stand up to parasites and periodic hard conditions, to snow, excessive sunshine, fires or drought. To do this work well we need plenty of animals, very good methods of registration, efficient fencing and an open eye for faults as well as for merits. It cannot be hurried, the number of generations required depends on the efficiency of the methods used and to some extent on mere good luck.

The Kleberg family corporation have had good luck and perseverance. A mating between a large mongrel Shorthorn-Brahmin bull and a cow of preponderantly Shorthorn ancestry gave an excellent red bull, "Monkey", who happened to be homozygous for very many things, and the best families all trace back to this individual bull "Monkey". A rare stroke of good luck.

The breed has been produced on the enormous Texas range property, to fit range conditions. In common with the Jersey,

the Afrikaander, and some Mediterranean and Zebu breeds, they can (and do) graze in the hot sun. They are rustlers, very resistant to Texan range conditions and Texan "bugs". It is quite possible they will fit into the semi-desert ranging conditions of tropical Queensland now they are being tried out there, and stand up to dingoes, bush-ticks, bushfires, crocodiles, infected muddy waterholes and drought, just as well as to range conditions in their native Texas brush.

It will be very interesting to watch. The only point a geneticist must make is that before Queensland-born calves have grown up under Queensland conditions, we cannot know this positively. We all hope they will, of course. The first Santa Gertrudis bulls auctioned must have brought stiff prices, and this is a partial compensation for the Kleberg venture and initiative. But even stiff prices paid are no certain indication of real merit of course. Right in Queensland I saw a real picture of a Hereford bull win a championship and being bought to improve range cattle, a bull who had been raised on a succession of Jersey nurse cows plus eggs, and who probably could not distinguish between alfalfa and saltbush, never having seen either plant grow!

The important point for meat-hungry England is to get plenty of beef from somewhere. In the Queensland semi-desert, outback country, where farms are measured in square miles, the Santa Gertrudis may well fit excellently, and keep up its calving percentage, and on the packing station hooks, grade as well as in Texas. The country is now swarming with all sorts of Zebu hybrids in this land without fences. Such hybrids are notoriously tricky and quicker than any horse foaled in Australia, and even a few hundred "Mickeys" may play ducks and drakes with any well-laid breeding plan. A major problem will be to stop bulls going through the fences and to catch all non-pedigree bullcalves before they are breeding.

The native Australian breeds such as the Illawarra and the Corriedale have this in common, that they have been free to really adapt themselves to Australian and New Zealand conditions, and that they do not suffer the periodic infusion of imported British breeding stock, adapted to lush pasture, constant rainfall and the feeding of concentrates.

It takes many generations to obtain reasonable purity. Isolation and in-breeding will do the trick, but we need large

numbers to make it possible to discard *groups* that do not stand up to this and to continue from the *groups* that do. Mr. Kleberg's King ranch, by having a hundred times as many animals and twenty times as many separate herds as the average cattle farmer, was able to hit upon one chance prepotent male like "Monkey", and to prove him as a sire when he *did* occur.

The point was raised in a newspaper discussion whether it is not a pity to relieve the British meat shortage by utilizing non-British material, however efficient. I should think that it is not good economics to refuse to use anything ready made and to start making it all over again, in such long-range things as making a novel breed of cattle for a special purpose, especially if one would like to see results not a century from now, but in as short a term as possible.

Let us hope this Texas breed will happen to fit as well in the Queensland cattle bush as the Dutch Friesian fits in England, the Spanish Merino in the Australian desert, the Bessarabian Karakul in south-west Africa and similar cases of what I would call pre-adaptation.

If a word of warning is needed it can be given in the form of a platitude : " the proof of the pudding is in the eating". To relieve the meat shortage of the world by utilizing hot deserts, the Santa Gertrudis may be a good solution. So for that matter may be the Afrikaander, the Pinzgaue or some Mediterranean breed. What is needed here are cautious and fair large-scale trials, rather than a "boom" in a breed, however promising.

Swine. Among the larger agricultural animals swine stand out because of their great fertility and early maturity. This should make the breeding of swine much easier and progress more rapid than in cattle or horses.

The great fertility of swine must also be one of the reasons why regular progeny-testing as a method of practical value has been used with swine earlier than with the other farm animals.

Progeny-testing in swine was first used in Denmark. The method used consists of sending representative groups of piglets to fattening stations, where the young animals are raised and slaughtered. In these stations great importance is attached to a favourable proportion between the amount of food ingested and the gain made. The young animals are judged again after being

killed, as in selecting swine the quality of the offspring is of prime importance.

The Danish system has been adopted in some other countries, and sometimes changes have been made in it. Two very important points should always be kept in mind. In the first place the group of offspring tested should constitute a fair random sample of the parents' children; and in the second place special precautions must be taken to find animals that give aberrant young.

When a boar gets good pigs, but in addition also a number of wasters, one may easily obtain a wholly wrong idea of his prepotency and value as a sire, if we allow the breeders to send six groups of four pigs each from among his progeny to the testing-stations. A boar that is heterozygous for very important genes will probably sire a certain number of aberrant pigs. If we allow the breeders to kill off those piglets, and send four pigs out of each litter to the tests, this gives us a wholly wrong picture of the value of the sire. Pig breeders are so used to finding one or two worthless piglets in a large litter, that they fail to recognize that a good system of progeny-testing would soon do away with this loss.

An excellent test of a boar's purity and breeding value is to mate him with a number of his own daughters and note the result.

In the chapter on progeny-testing is discussed the importance of choosing between progeny-testing and selection for fancied correlative qualities, and of discontinuing this last kind of selection when we decide to use the progeny-test as a basis.

It is important that a large proportion of the breeding boars shall be tested as sires, not just a few of the finest-looking ones. The fact that the standard of points changes rapidly in the same breed of swine shows that the judges have no clear picture of what external qualities give a good promise of breeding value.

In many countries are kept breeds of swine that differ very little in average butchering value. Swine breeders should realize, however, that similarity in quality gives no guarantee of genetic identity. Hybrids between two such breeds are likely to be very impure, heterozygous for a great many genes, and such hybrids, no matter what their personal quality may be, should never be indiscriminately introduced as breeders among one of the pure breeds. If it is desirable to resort to a cross between breeds, the hybrids should be mated back and back to

the breed we want to improve, six or seven times, before we declare the back-crossed progeny to be worth taking up into the breed.

In many instances with swine, first-generation cross-breds have excellent qualities. In Denmark a great proportion of the pigs produced are bred from Large White crossed with the Danish Landrace. This is a very good system, as long as breeders recognize that the hybrids must not be used for breeding. The theoretical explanation of the good quality of first-generation hybrids is given in a special Chapter.

Swine breeders should realize that it is quite possible for wild species of swine to carry inherited factors that might conceivably be of great value if introduced into our present breeds, even if the combination of all the genes in such wild species may not give us very good animals from an economic standpoint. I have already referred to the disease-resistance due to a cross with the European wild boar. Experiment stations should test out this and other species of swine by testing the quality of animals derived from back-crosses of hybrids back to domestic breeds.

Sheep. Sheep are kept in the most diverse climates and circumstances, and local breeds are always adapted to these circumstances—very small sheep in the desert, large, quickly-maturing breeds in places with very good pasture. The average fertility of a breed of sheep must also be adapted to its surroundings, the sheep producing most lambs being found in very fertile country.

When conditions of agriculture change, it may be necessary and profitable to change over to a different breed of sheep, and this can be done by grading over. Where much cross-breeding has resulted in a very mixed population, selection supplemented with test-mating will make a homogeneous breed of it.

On the island of Texel in Holland the local sheep were small, with a short pointed tail. Rams of different breeds, Lincoln, Wensleydale and others were imported, and an export trade in early lambs sprang up. When I first visited the island in 1910 the sheep of Texel presented a very heterogeneous aspect, especially before the lambs were weeded out. I advised stopping the importation of different rams and making one breed of the best animals present, using progeny-testing of males as an aid

to selection. It was surprising to notice how soon a semblance of uniformity was arrived at. At present this is the best breed of sheep in Holland, and the Texel sheep is as pure as most old English breeds.

In sheep the practice of crossing different breeds is more prevalent than in any other domestic animal. Sometimes the cross-breeding produces excellent fertile ewes, good milkers, and these are used to produce lambs from yet another breed. The cross-bred ewes are often a very uniform lot, but as they are heterozygous for many genes, their offspring is always more or less variable, which is sometimes not very important when the average quality is good.

Sheep differ enormously in inborn resistance to disease. Before trying to "improve" a local breed or change it over into a more valuable one, it is always well to discover whether this new breed really can thrive under those local conditions, and to do this the new breed must be tried in its pure form.

The idea that in sheep hybrids will breed true to type is a fable. Wherever hybrid sheep are bred from, a very great variability results. We can mask a great deal of this variability by weeding out about half of the lambs, and to see the real picture it is necessary for the investigator to inspect the flocks before this is done.

Fertility in sheep is greatly influenced by environment. When small sheep from semi-arid climates are brought to good pastures or fed well, they are sometimes amazingly fertile. A small group of black-headed dwarf Abyssinian sheep at the London Zoo used to lamb down twice a year regularly and produce very large litters of lambs, so that the group multiplied like rabbits. It is probable that this innate tendency to great fertility made it possible for the sheep to breed at all in their natural habitat.

The Dog. Most breeders of dogs breed show dogs. In many respects the breeding of dogs for the shows differs fundamentally from the breeding of dogs for practical use. The breeders of hunting-dogs must try to work in such a way that few aberrant dogs are produced, as the real quality of their dogs is not apparent until they are grown up. The same is true of the breeder of sheep-dogs, and of other dogs that are valued because of their intelligence.

The breeder of show dogs is not bound to work in such a way

that he produces a uniform lot of dogs. In fact, this would defeat his object, which is competition at the shows between the looks of his animals and those of a competing dog. To win at the shows he must try to breed a few animals that are just a little better than the other man's dogs, and this process can never end, because as soon as the ideal of the show standard is approached, it recedes. Show standards change continually, they are wholly a matter of fashion, in fact the change of show standards takes place in a way exactly comparable to the changing of fashions in ladies' clothes.

It is not necessary that all dogs produced shall be good; it is much more important that one or two superlatively good ones shall occasionally be produced. In fact, sometimes the dictates of the fancy make it impossible to produce a pure strain of dogs. One of the most curious instances is that of the breeding of small toy dogs, like the Yorkshire terrier. In those breeds some of the miniature males, good enough for showing, are quite fertile. The miniature bitches are too small. For this reason the breeder mates the small males with largish females, that have been bred from miniature fathers. Such matings produce largish and miniature, both males and females. Of these pups, the miniature pups are the ones from among which the breeder selects his show specimens. The largish bitches, when they have excellent coats and other points, can be used for breeding, and the largish dogs are not used.

The same state of things was found in the Toy Pincher, when very small individuals were the fashion. The shows call for somewhat less extremely small dogs now in this breed, but of course miniature pups (small being recessive) are still being produced.

Dog breeders are continually resorting to cross-breeding in order to improve certain points in their dogs that happen to have the special attention of the judges at the time. Almost immediately after our Dutch Keeshond was imported into England, breeders crossed it with Chows and with Elkhounds, to produce some variability that would permit further improvement by selection. Dog breeders made the Airedale terrier larger by the use of Gordon Setters, and recently they seem to have worked in some other cross, which has resulted in so many of the recent prizewinners showing a sort of ridiculous mincing Hackney leg-movement.

There is one special instance in which cross-breeding could be profitably used, namely, the breeding of erect ears into those dogs that used to be shown with cropped ears, notably in the great Dane, the Boxer and the Schnauzer. It would be quite feasible to produce erect ears in such breeds in about three to five generations. To this end a dog of such a breed should be mated with a specimen of a breed with standing ears. It is not really important that this should be a closely-related breed. I would expect the mongrel puppies to have standing ears, or tipped ones. The next step would be to cross one of the mongrels back to our breed. This would give pups of which only one-half would have erect ears. One of these should be re-mated with the breed to be changed, and this process should be repeated. The only thing necessary is to take care that in every generation only an animal with standing ears is chosen. Contrary to expectation, this would not result in a smaller and smaller proportion of pups with pricked ears. With every generation the dogs would become more like the original breed, and in about five back-crosses the animals would probably be enough like good specimens of the breed to begin breeding them together to get the real stiff-standing ears of the homozygotes.

I can heartily recommend this process to any good breeder with sufficient perseverance to keep at it until complete success is reached. It would of course be advisable for a breeder to work in co-operation with a geneticist. I think it would be easier to do the work quicker in some breeds than in others; I would not be surprised if it could be done in three to four years with the Schnauzer.

Although at first sight it would appear as if the show breeder could safely let the mentality of the dogs take care of itself, because winning at the shows is a matter of producing the fashionable dog and not the intelligent or the good-tempered one, this is not wholly true.

When the Collie breeders crossed with Borzoi to make the skull long and narrow, they worked exclusively for the shows and neglected to weed out the treacherous or stupid dogs. The result has been a very great success as far as the show is concerned, but at the same time the breed has lost caste as a popular house-dog, and for this reason it had to make room for nicer dogs. After all, even a show dog must float on the support a great many enthusiastic owners of house-dogs give to the

breed, and these people look for an intelligent, good-tempered and alert dog.

For some reason that I cannot understand, dog breeders seem to be especially subject to the invention of fancy theories about inheritance. I remember a very curious case in which a man proposed a theory according to which it was practically unnecessary to regard the female ancestors of a male fox terrier, or the male ancestors of a bitch. Even to-day there are breeders who believe that the pups inherit colour from the father and shape from the mother, or vice versa. It may be added that a bitch, when bred to two males, may give a mixed litter of which some pups are produced from sperm of one male and the others from the sperm of the other. Even in such circumstances the pure-bred and mongrel pups in one litter do not influence each other.

Size of the pups is influenced more by the genetic make-up of the pups than by the size of the mother. I found that in a litter the pups that are heaviest at birth generally remain the largest, and vice versa. I once tried to make a breed of miniature Dachshunds by hybridizing a 3-lb. Toy Terrier with a Dachshund bitch. In this case small size happened to be dominant, so that the pups remained very small. This was extremely unlucky, for when I bred the hybrids *inter se* to produce the desired re-combination of factors, both bitches died at the time of the birth of their second litters when an extra large pup could not be born.

Most novel breeds are simply imported. It would, of course, be possible to produce wholly new breeds by cross-breeding. In some instances extremely beautiful and attractive dogs can be produced as first-generation hybrids between two old breeds. If I happened to live in England, the dog breeder's paradise, I would once more cross the Chow with a red or sable Collie, and invent some good name for the hybrids. I am sure that if I were to describe those strikingly beautiful hybrids, with very long hair standing out, and with an affectionate disposition, as "Mesopotamian" or "Patagonian" dogs, they would produce a sensation!

The dog can be crossed with several different wild species. Hybrids between wolf and dog, jackal and dog, and fox and dog, have been bred, and all the hybrids are fertile. One of my friends in Holland has recently bred two litters of very useful

wolf-dog hybrids. Notwithstanding the recent campaign to hush up the introduction of wolf genes into the German sheepdog, which was started by the fear that the idea would give the breed a bad name, it can easily be proved that just about the time the German sheepdog was being used as a police dog, hybrids with wolves were produced and utilized. It is probable that some of the excellent qualities of the breed, its unquestioning obedience, its exemplary mastery of self, are due to the cross. I have had a pet wolf for some time, and I know that in many respects a well-trained wolf is superior to almost any dog.

In certain quarters there is some doubt about the dog-fox cross. The two instances I know of, however, seem to be very trustworthy. It would be very interesting if someone tried again to obtain such hybrids. It may be useful to record that in both instances mentioned, the cross was made between a vixen and a male dog, and, strange to say, both in the German case and the French one, the mating took place in August!

The cross would be of great value to fox breeders, as the dog has several qualities that it would be extremely useful to have in foxes, namely, its tameness, fertility, and disease-resistance.

Dogs to Lead the Blind. The ordinary methods of selection are not well suited to the case of dogs destined for leading the blind, for, both in bitches and in dogs, breeding interferes with the work the animals are doing. It would be like putting a blind person's eyes out to immobilize him at the bedside of a bitch with a litter. And breeding from close relatives of the very best dogs is certainly not the best way out of the difficulty.

The point is, that even in the purest of available breeds, too many dogs are born that are useless because they are lacking in genes for which their parents happen to be heterozygous. This is true in visible traits, but it is certainly also true in respect to the subtle psychological qualities that make a dog suitable for such work as herding, and perhaps even more so for the very special work of leading a blind person.

If we could find one breed ready-made for the purpose, this would be ideal. But too many dogs of a suitable age that are given or sold to the training centres have to be returned to the man or woman who raised them. This is a double tragedy, it is a waste of effort and money spent on training the animals and I am afraid many of the dogs rejected find their way to some

laboratory, a purposc for which the owner surely did not intend them.

To have a continuous supply of trainable pups, no matter whether these are specially bred for the purpose or just bought in or obtained by donations, without the present appalling percentage of rejects (40 to 50 per cent.) there would be two methods. One would be to breed a strain of dogs of great purity, and the other would be to utilize first-generation hybrids, like so many breeders of other animals do, breeders of lambs, chickens or beef cattle. The second way is certainly much more promising.

To have a continuous supply of trainable pups, finding two very good but different breeds that "nick" together is the method that seems the very safest. What the ideal combination of two breeds will turn out to be is in the lap of the gods. If I hazard a guess it would appear that the Border Collie must be one, and some quite different breed, also bred for use and not spoilt by showing, must be found that will "nick".

I was very lucky to obtain for Holland some very excellent Border Collie pups of sheepdog trial fame from Miss Currie in the Isle of Arran. It is the intention to try combinations with other breeds, and the Boxer or Retriever seem indicated. The only pup of the original litter of Collies tried, turned out to be a first-class Guide Dog.

From the original cross between an Alsatian and a wolf, one enthusiastic breeder (see Fig. 27) is trying to breed an inbred strain of dogs to lead the blind; he has certainly furnished a good many blind persons with very good dogs. But of course it will take a good many generations for this group of animals to breed true to type.

In conclusion, I might add that the first-generation hybrids I am considering, between two strains that "nick", must be trainable by the sort of trainers we are likely to find available to-day. Some dogs, like the Alsatian, stand some rough treatment that would immediately spoil a sensitive dog like the Border Collie.

It does not matter at all if a trained Guide Dog is personally heterozygous for the many genes that combine to give him or her the very good psychological qualities we want, the dogs are meant to be used, not to be bred from. When I saw Captain Liakhoff's work at the Leamington Spa training centre, some of the most promising dogs in training were hybrids.

Personally I am convinced that the height of the dogs of one of the two breeds to be kept apart and combined is very unimportant. The Keeshond makes an excellent Guide Dog, and so, undoubtedly, would most Corgies.

The Cat. Cat breeders are interested only in showing; there is no interest whatever in breeding cats for any useful purpose. The oft-repeated story that important farms of black cats exist in Holland is a fable which depends upon the circumstance that Holland really is an important collecting-centre for cats, moles, and fitch skins. The black cat-fur Holland produces is collected by thieves, poachers and game-wardens, who make a specialty of killing other people's cats for the sake of a few pennies, just as is done elsewhere.

Very few breeds of cats are bred for the shows in Western Europe and America. The genetics of the colours in Persians and short-hair cats is now well understood. From a genetic standpoint the inheritance of tortoiseshell is very remarkable, because hardly any fertile males of this colour are produced. So far, Siamese are recognized at the shows in two colours only, although new colours could of course be easily produced by cross-breeding.

In breeding Siamese it might be worth while to bring in one or two genes to protect the animals against infections to which they are now extremely susceptible. Hybrid Siamese are not particularly delicate.

Very rarely new breeds are introduced and shown, and some of the so-called introduced breeds are of doubtful origin. I suspect the Blue Russians to be produced from cross-breeding with Siamese; the circumstance that blue-pointed Siamese turned up in England at about the same time as Russians seems significant.

The nearly unmarked Abyssinians could be turned to account to produce beautiful Chinchillas if anyone had the ambition to do this, and by the aid of the Abyssinian a really unmarked orange Persian could be constructed.* Manx cats somehow never became very popular. Many promising breeds or single characters might be imported into countries where cat shows are kept. I have never yet seen at the shows a cat with drop-ears,

* During the second world war Professor Haldane bred a few solid orange males according to this "recipe".

such as can be met in China, or one with the extremely short "Rex" fur, such as one sometimes sees in Java. A cat of this description was described from America in the *Journal of Heredity*.

Cat breeders are very apt to use out-crosses, probably unnecessarily so, as in-breeding in this group is probably just as necessary to produce animals of great size as in other stock. Especially where one exceptionally good animal is found, breeding back this specimen with its daughter and granddaughter (or son and grandson, in the case of a queen) should be resorted to to try to duplicate the excellent specimen.

Several wild species of cats exist that could be tried in species crosses with domestic cats. This work is very promising from a show breeder's standpoint, for not only would it be possible to combine the larger or much smaller size of different species with the colours of domestic cats, but it is extremely probable that many wholly novel characters would turn up in the second generation from fertile hybrids.

The Rabbit. The great majority of rabbit breeders are breeders for show. Rabbit pelts must be considered as a by-product of the rabbit-fancy. In several of the preceding chapters the problems that confront the show-breeder are rather extensively discussed.

In the breeding of rabbits inherited quality counts for very much, and preparation of animals for the shows is reduced to the very minimum. Show animals must be trained, especially in such breeds as the Belgian hare, and they must be shown in good coat condition, but for the rest the best animal really wins.

There is one quality in rabbits, however, which is greatly influenced by environmental conditions, and this is size. In the giant breeds, such as the Belgian, it pays to give the baby rabbits a good start, and for this reason foster-mothers are indicated, two babies to the mother. In the dwarf breeds, the reverse is true. It does not do to starve the animals, but as especially the Polish does are very little fertile and tend to produce very small litters, it is a good scheme to give them a few other young rabbits to nurse in addition to their own.

In rabbits more than in any other animal I know, excepting fur animals, the breeding of many breeds tends to run to "booms". When the enthusiastic breeders of a newly-imported

or newly-made breed succeed in making other people believe that this breed is especially valuable, prices of breeding stock tend to soar. New people buy expensive breeding stock with the intention of selling their own young rabbits at a slightly lower price, and this goes on until the breed is spread all over the country and no demand is left to take up the over-production of young breeding stock. One who has witnessed several Belgian Hare "booms" in America, an Angora "craze" succeeded by a "Chinchilla boom" becomes very sceptical whenever the merits of a new breed are lauded. If making other people believe in the enormous value of expensive breeding stock is the only way to make money in breeding rabbits, this is a very poor sort of business indeed!

It is extremely problematical whether the keeping of rabbits for meat, for fur, or for wool, ever pays. When the price of rabbit-wool is high, the production of wool is perhaps profitable, but a small fluctuation in the price of wool is sufficient to make the profit disappear.

The breeding of very fine show rabbits is an excellent hobby, and clever breeders make it pay by studying the way the fashion changes, when it tends to do so, which is more seldom in rabbits than with other similar livestock.

Rabbits can be cross-bred with hares. The resulting hybrids, "leporids", are always similar, just as mules show a very great resemblance, no matter what the quality of the mare has been. Leporids look like coarse grey rabbits with fleshy ears—there is nothing hare-like about them. This fact has made very many people disbelieve in the fact that they can be produced; they think the breeders must be mistaken, and that the rabbit which was thought to be mated to the hare was previously mated to a rabbit.

I can vouch for the truth of the existence of leporids; I have owned several, and I have carefully compared many litters. The former director of the Rotterdam Zoological Gardens, Dr. Kuiper, bred a litter of hybrids from a male hare and a female Angora rabbit. I bought a lop-eared female rabbit once, after she was seen to mate with a wild hare, and I owned the hybrids. Later I knew a man who had a pet doe hare in a hutch; it was mated to rabbit males three times in succession, and produced a litter of hybrids every time. One of these times I saw the doe hare when she was heavy in young, and again

three days later, when she had produced her three hybrid babies, that were fully-furred and born with open eyes after a period of gestation of more than five weeks. Two of those young rabbits were kept by me for several years, and like all the other leporids seen by me they were perfectly fertile.

I cannot account for the failure of some of my colleagues to produce leporids. The best way to do it again is to use a female hare, as this obviates the possibility of a mistake. If a female hare produces something which looks like a coarse rabbit with yellowish eyes, it is impossible to believe these young are from an accidental mating.

Curiously enough, all the leporids I have ever handled were easily tameable. Hybrids between tame and wild rabbits, however, are quite wild. The first leporids reported were bred in France by Perier after very many unsuccessful attempts. This cross was made at a time when hardly any domestic rabbits existed, and the animals crossed were wild hares and wild rabbits. His description of the hybrids fits mine. There is every reason to believe that these first leporids have helped to produce tame rabbits of the larger breeds in France.

Bancroft in Berkeley (California) bred leporids between a tame rabbit and the Californian jackrabbit, a large hare. I do not know whether those hybrids were tested for fertility.

If leporids can be successfully mated back to hares, as well as to rabbits and *inter se*, it might be possible to produce a breed of animals which, for all practical purposes, would be a hare that could be produced in rabbit-hutches. The Belgian hare is a breed of rabbits, but the possibility is not excluded that the hare contributed to its genotype. When bred to one of these Belgian hares, one of our leporid does gave as many reddish as grey young, but there was nothing hare-like about them.

I have tried mating domestic rabbits with the miniature Californian brush-rabbits, but without success: the cannibalistic tendency in this wild species has made such matings impossible.

Poultry. Poultry breeders, probably because they have much more experience than the breeders of larger domestic animals, generally have a better understanding of the scientific principles underlying their methods, and as they are more likely than cattle breeders or horse breeders to make their living exclusively from their activity as breeders, they are more likely to ask the

help of the specialist geneticist to help them solve their problems. This is one of the reasons why I have co-operated more often with poultry breeders than with breeders of any other kind of livestock, barring sheep.

Most of the larger chapters in this book contain references to poultry and poultry breeding, both the breeding of show birds and utility stock. It is not therefore here necessary to do more than elaborate some of the points treated of, where this is absolutely necessary.

In the breeding of egg-laying breeds, the only system of selection that has been proved to be successful is that of selection in the male line according to the average quality of the daughters of the males. In other chapters I have given the genetic reasons for the adoption of this method, which I have taught to several breeders of fowls and ducks, so that it will be sufficient merely to give the bare method.

A number of males of good parentage are mated, each to a number of females, and the eggs from those matings are all hatched at one time. The chicks when hatched are wing-marked or toe-punched, so that it will be possible to find which male was the father of each chick. Chicks of different mothers in one pen are not kept separately.

When the pullets grow up they are housed in groups, each composed of the daughters of one father. Males are kept from all the different sires. The quality of each group of daughters is fully tested. The eggs are regularly counted and weighed, the mortality in each group is noted, the food consumption is regularly checked, so that at the end of the season it is possible to know which group of birds has given the greatest amount of profit. This group is chosen as the breeding stock for the next generation. When culling is unavoidable, because some pullets are ill or deformed, or obvious non-producers, the records of these culls are not rejected, but they help to lower the average quality of the group in which the culls are found. This is necessary to find out whether selection really has the desired effect.

Next season the selected group of young birds is mated up, half-brothers with half-sisters, so that each male is again mated to an average group of females. This process is repeated in every subsequent generation. This programme entails some mild inbreeding, and for this reason it is necessary that in every generation only the very best group is chosen, and that no points of

value are left out of consideration. If in any generation none of the groups are good enough in the opinion of the breeder, the males of one group are mated to the females of another, choosing the two best groups.

In practice it is found that in every special case details have to be arranged to suit it. This is a matter of discussion between the breeder and the consulting geneticist who should have some experience in these matters.

The fact that in different respects certain combinations of breeds give hybrids that are superior in practical value to the pure breeds crossed, makes it probable that it would be possible to produce new breeds of poultry that would be superior to the ones we now have. In our existing breeds all we can hope to attain is the best possible combination of the genes present in the breed, and the question may be asked whether this is really the very best that can be done.

In the breeding of plants it often happens that progress is possible up to a certain point, after which new sources of valuable genes must be sought. In poultry breeding it would probably be possible deliberately to make one or two new breeds by selection in a very variable population of birds produced by breeding hybrids between two different breeds *inter se.* From experience in this sort of work I know that such an undertaking should never be on a small scale; the variability produced by crossing even two related breeds is so enormous that one easily misses the very best individuals if his group is insufficiently large at the start.

In England it would certainly pay to produce a good, quick-maturing, white-skinned table-fowl, something on the lines of the excellent hybrids between North Holland Blues and Cornish Game, with sufficient fertility.

Breeders of exhibition poultry on the look-out for novelties should try out the possibilities of cross-breeding with the wild *Gallus furcatus.* Hybrids between males of this species and domestic hens are regularly produced on some of the islands around Java by a system of tricking the monogamous males into treading a pegged-down hen. It could easily be done by means of artificial insemination. The hybrids, called "bekisar" in Malay, are very popular in the East, because of the way they crow. Such hybrids, which are monogamous like their father, are fertile, and from such males and domestic hens some of the

most surprisingly coloured poultry are produced, mostly by Chinese fanciers. I have seen a bluish male with a vivid gloss that can only be described as pink, and some animals with green and yellow in the comb, and with the medium wattle of *G. furcatus.*

African Game Farms. Some of the rarer African big-game animals, such as the Eland, an enormous antelope, the Gemsbok, the Whitetailed Gnu (Wildebees) and the lovely Springbok, are in real danger of dying out outside of the game reserves. They can all be bred in enclosures. The way to make really new domestic animals out of this material would be to cross local species, especially in the Eland, and select for high tameability in the following generations.

Both in the Union and in south-west Africa, my attention was drawn to the fact that the ruling that permits the sale of surplus animals from such private game reserves is sometimes abused by men shooting game for the market in large numbers, and covering this nefarious practice by having a relatively small number of enclosed beasts in a registered "game farm". When a man markets great numbers of game from a limited area his licence should be investigated.

Chapter Forty

Breeding of Special Groups of Animals—II

The Buffalo. Buffaloes thrive under circumstances in which other cattle could not exist, but as they have very special requirements and very special drawbacks they are only utilized in a few countries. They need a place to wallow, and they are awkward to handle on the road in heavy traffic, they may go berserk with very little provocation, but at the same time they do produce the cheapest meat and labour and butter of any large domestic animal I know.

For extremely heavy traction, for dragging out tree trunks by main strength, for producing cheap meat in marshy country, the buffalo is unexcelled. In countries where the buffalo can possibly be kept, the problem of economic milk production is easily solved, provided one of the special British Indian curved-horned milk breeds is chosen. These animals turn rushes and straw into milk at an astonishing rate.

In North Australia, where buffaloes have run wild and where only the hides of the hunted animals are utilized, the possibility is not excluded that in some spots grading this stock over into a milk-producing and more docile breed might pay very well indeed.

The European breeds are mostly used for work only, but keeping milking buffaloes in the same places would be worth trying.

The largest breeds are found in tropical countries, and different islands in the Philippines and in the Java Seas are apt to have each their own local breed. In Java many albino caraboa are bred, and in Celebes a holy breed of spotted buffalo used in religious ceremonies is kept.

The buffalo is an unpleasant animal with a very spotty temper, but in these days when farmers in Europe are turning to

camels, where these can be used more profitably than horses, it might be worth while to investigate the economic possibilities of some of the better breeds of buffaloes, even in countries where agriculture is at a very high level.

The Goat. Goats are generally kept for the same purposes as sheep, for hair and skins, for meat, for work and for milk. In one country milk may be of chief importance, and meat may come next; in other countries the milk is never utilized.

Goats can be kept as a supply of meat cheaper than almost any animals, and this is especially true in densely-populated countries, where every scrap of food is utilized, and every square foot of land is cultivated. The small goats in Java that browse along the galangans between the rice fields, and do not hesitate to climb a tree to find something to eat, provide very cheap meat for their poor owners. The smaller the goat the better, under these circumstances, as I have explained at some length in another chapter.

In semi-arid regions, such as in parts of New Mexico, in Mexico and South Africa, Angora goats are kept for the hair. In this instance at least it is possible to determine the merit of both sexes, as the males can be shorn and the fleece weighed and examined for kemp. To establish the Angora goat industry in a country full of other goats it is not necessary to import large herds of good Angoras; it is sufficient to import a small herd to provide high-grade males for grading purposes. Cross-bred goats have shortish hair, but after three or four matings to pure-bred males, the later generations begin to be good woollers. This process of continued breeding back to pure-bred males should not be considered as finished too soon, it is better to go on with it too long than to keep too much of the impurity in the new herds. With this as in all similar cases of grading one breed into another, it is very important that we should have a quick succession of generations. For this reason it is important to separate the animals of the fourth generation from those of preceding generations, so that we do not mistake kids of the does from earlier generations for those with "a higher proportion of Angora blood". It has been proposed to produce polled Angora goats, which would be quite easy (see the chapter on adding a gene) but inadvisable in countries infested by coyotes, jackals or similar predatory animals.

The work done by goats does not amount to very much. In the south of Sumatra one sees goat-carts in use for light transportation, and the same use is made of goats in other islands of the archipelago.

In Europe the goat is essentially a milk producer. In Switzerland the villagers keep goats in the villages to provide themselves with milk during the time the cows are up on the Alps. For this purpose they need a goat that will produce a great amount of milk when fed on excellent food, even if the lactation period does not last very long. The Toggenburg and Saanen goats fit these requirements excellently.

It is very important always to keep in mind the purpose for which we need an animal. In another chapter I discussed the disastrous results of a scheme to improve the small labourers' goats by crossing with Swiss goats. If goats are to be kept as cheaply as possible for milk production for the family, two things are essential, the kids must stand being bred in their first autumn, and the goat must keep in milk for a very long period. A goat that continues to give two quarts of milk a day for almost the whole year, at very little expenditure, is better than another one that yields more gallons of milk in the year, but gives all the milk in seven months.

The goat-breeding centre at Serooskerke in Zeeland, Holland, is an excellent example of the breeding of animals for economic production. Here males are tested according to the production of daughters that will produce milk cheaply, and hired out to breeding centres.

The Ferret. The ferret has long been thought to be an albino variety of the European fitch. This is probably not true. In the first place the ferret is not an albino; it could be more properly described as a pink-eyed cream or fawn. This can be seen by comparing so-called white ferrets with albino rats and with pink-eyed cream rats. Also, even the palest cream ferrets sometimes carry a white blaze, or a white spot on the forehead, such as would not be visible in true albinos. Some of the yellowest ferrets show a distinct pattern, similar to that of the black-eyed specimen, with a transverse band across the face and a distinctly darker belly.

In the second place the ferret is certainly not a fitch. It differs from the fitch in several ways. Even the darkest ferrets have

whitish underfur, not orange-yellow. They are generally much more long and slender. Their disposition is different; they are much slower in all their movements than even the tamest of tamed fitches, they are not easily frightened, and do not use their anal glands. A curious difference which makes the ferret adapted to breeding in captivity is the striking swelling of the vulva in the females in heat. This quality makes it possible to breed ferrets even when each owner has only one or two animals, as this sign of breeding condition cannot be overlooked. The ferret thrives on a diet of bread and milk with a very small piece of meat occasionally, and on this same diet a fitch (polecat) rapidly starves.

It is hardly believable that anybody would ever dream of taming the fitch to take it rabbiting; to anyone who has ever kept tame fitches this sounds like going hunting with a pet tiger! Even the tamest fitch is extremely quick and snappy ; it is certainly not to be trusted loose.

It is probable that the first animal to be tamed and used for ferreting has been the related Siberian fitch, which differs very much from the European one in disposition, colour and shape.

Never having bred these animals myself, I do not know whether the food requirements differ from those of the black fitch, though this is not probable. As far as I know, no attempt has ever been made to hybridize the two species, but it would be extremely interesting to try this, to find out whether selection in the second and third generations would produce tame or ferret-coloured individuals.

I have succeeded in inducing both the stone marten and the ermine to copulate with female ferrets, but without results. It is probable that the so-called stoat-ferrets, suitable for ratting, are simply small young females, possibly of specially selected small strains.

Ferrets vary enormously in every respect. I have had baby ferrets (in hybridized lots) that opened the eyes as early as at three weeks of age, instead of the usual five. The babies often varied much in the size of the tough patch of skin that is "vulcanized" into the spot by which the mother grasps it in carrying. The length of the tail is very variable in some families. By hybridizing ferret and European fitch beautiful first-generation hybrids are produced, having food requirements somewhat less strict than in the wild species, and very valuable pelts. These

hybrids were less susceptible to distemper than fitches, but seemed more susceptible than ferrets.

Ferrets are extensively used nowadays for experiments on distemper, and in the production of vaccines. They vary much in susceptibility and comparative immunity, and it would be very much worth while to select special strains for this purpose.

Fur Animals. The breeders of fur animals aim to produce pelts that are at least as valuable as the pelts of trapped animals. In general it is not desirable to change or improve the pelts; the problems confronting this group of breeders are almost wholly domestication problems.

Most of the fur animals, such as they exist in nature, will not readily reproduce in cages. The skunk is a notable exception, as this animal, even if caught up as an adult, will breed readily.

Some of the fur animals, such as the mink and the fitch, will only breed when raised in the pen from early infancy. When I started with fitches, I bought over thirty females caught wild, and never succeeded in having one come in heat in the cage, but cage-born young were found to breed readily on the same diet.

There are two ways of obtaining success in the breeding of fur animals in cages: we can either adapt the cages and the diet to the animals, or we can try to change the animal so that it will breed readily in an economically-made cage on a cheapish diet. We are here concerned with the latter problem.

With a few animals there is the possibility of utilizing a domestic animal to ameliorate a wild fur-bearer. The fitch will readily cross with the domestic ferret, and the hybrids are fully fertile. From such hybrids I have produced a few animals that were as tame as ferrets, and that did not need a more elaborate diet than ferrets, but that had as beautiful a pelt as the wild dark fitch.

The fox has been successfully crossed with the domestic dog, and the hybrids are fully fertile. Such hybrids can be mated back to foxes and it seems quite possible to introduce some of the good points of the dog into our present breeds of silver foxes. I know of a silver fox bitch with a curled tail that barked like a dog, and almost certainly had a dog among its ancestors.*

The present strains of silver foxes have been produced by

* The owner in Quebec told me this story when I visited his farm there in 1927.

cross-breeding different silvers caught wild, notably black sports of the Alaskan and of the Eastern fox. The silver or black fox is a recessive compared to the wild red animal, but the two blacks named are different recessives. Hybrids between Alaskan and Eastern silver foxes are not black but so-called "cross" foxes that will give many silvers in their descendants. I am convinced that the domestication of the silver fox has been due to a great extent to selection for fertility, adaptation to captivity, and to cheap food under the very variable descendants of such hybrids. The process has been an unconscious one, but this sort of work could easily be done deliberately at present. The same is true of the mink and the fitch. In both of these at least two wild species exist, the American and European mink and the European and Asiatic fitch. Species-crosses would surely give very much variability and the possibility of selecting for greater gentleness and easier food requirements. The same thing is true of the ermine and of the raccoon. The idea that breeding a wild animal in captivity for a number of generations would domesticate it, in the absence of cross-breeding, has been treated in the chapter on domestication. Fur breeders should also carefully read the chapter on in-breeding.

Material success with fur animals comes both from improving the quality of the fur of the animals, and from the sale of breeding stock. Some fur animals are impossible as a source of profit when the sale of pelts is the only thing that brings in money. It is quite impossible to breed raccoons in cages, keep the young for eighteen months, and then compete with the trappers who catch wild ones; but selling young raccoons, especially black ones, as breeding stock may pay very well. Good prices can be obtained for breeding stock when the breeder can make his customers believe that the animals are profitable to breed for the pelts. In the first ten years of silver fox farming the chief asset of a breeder was an aptitude for smart salesmanship. The ridiculous over-capitalization of fox farms could only be compensated for by "passing the buck" to beginners.

A legitimate source of profit is the sale of breeding stock in a species that has not been bred in captivity before. By being the first man to breed fitches in captivity, I earned some money long ago from the sale of cage-bred young stock. The same thing could be done with martens and ermine by anyone with sufficient perseverance.

The most profitable fur animals are those belonging to varieties, that are not found plentifully in nature. The great value of the silver fox is due to this. Whether it will pay in the end to breed black and albino raccoons, colour varieties in mink and yellow skunks, will depend upon the willingness of the fur market to pay a stiff price for the aberrantly coloured pelts. Breeders should not mistake the temporary high prices of breeding stock in such freaks, which makes their culture profitable for a few years, for a sure sign of real value.

Wild Animals. In the chapter on domestication has been discussed the origin of domestic animals from wild ones. Cross-breeding between species causes genetic variability, and this variability makes it possible to produce novel combinations of genes, and new breeds, adapted to special needs.

Every group of domestic animals or birds is always found to be related to some wild species which, just as it occurs in nature, happens to have the hereditary make-up that allows of its being tamed. This points to the probability that, in every group, this tameable species has been the one taken into cultivation first, crossing with other species furnishing the variability. If we remember that most of our domestic animals were domesticated by relatively primitive people, it is clear that this must have been the only way in which domestic animals ever could get a start.

In the group of ducks the mallard is readily tameable, in the dog it is the wolf, in the swine most wild species are tameable. The wild rabbit is not tameable as a rule, but the hare is, and so are the hybrids. In cattle the banteng is readily tameable, and so are the wild relatives of the horse and donkey.

It is not true that in order to produce tameable domestic animals at least one of the parent species must itself be tameable. In my own crossing experiments with wild rats, such as the European black house-rat, the Egyptian house-rat and the tree-rat, animals that are wholly untameable even if taken in hand at an early age, it was possible to obtain real domestic animals by breeding from the hybrids and (mostly unconscious) selection of the rats that were tamest and bred most easily in small cages.

Making these domestic animals from two untameable species was possible in this instance, because we succeeded in breeding the wild animals in strong, suitable cages. It is evident that this

process could never be expected to yield a success in the hands of primitive man. It is also evident, however, that now we know that we can hope to get tameable animals by cross-breeding wholly untractable wild species in cages and selecting from the second generation, we could probably duplicate what we have done with rats with other animals.

This is one of the most promising tasks of the zoological gardens. If the zoological gardens can breed large F_2 generations from hybrids between buffalo and wisent, it is clear that from such material a new useful domestic animal may be produced, suitable for special conditions where domestic cattle would not thrive.

Wherever there is a market for wild animals, it is worth while trying whether breeding them pays, and wherever this is true, cross-breeding between species or sub-species is indicated, in order to produce the necessary genetic variation for selection to work upon.

The breeding of gamebirds can only be made to pay when methods are found to propagate the birds in captivity in sufficient numbers economically. A significant difference between domestic gallinaceous birds and domestic ducks on the one hand and wild species on the other lies in the polygamy of the domestic breeds. It is very probable that in such birds as the European partridges and in the American quail and bobwhites inter-crossing closely-related species or sub-species would quickly give us very variable groups, in which polygamy would also be found in some of the males. A likely cross would be that between the Californian valley and mountain quails, as the hybrids are said to be fertile. In these quails and partridges, the monogamy now makes it necessary to keep every pair in a separate enclosure, whereas polygamous males could be kept with a large number of mates.

Hares can be bred in enclosures. It would probably pay to produce an animal that would combine the obvious qualities of the hare with the ease of reproduction and superior fertility of the rabbit by taking leporids as the starting-point.

In ornamental waterfowl, such as wood-ducks, interspecific crosses might produce polygamy, just as it has done in domestic poultry, and this would make reproduction more economical.

There are few amphibia and reptiles that are bred in captivity. The axolotl might almost be numbered among the laboratory

animals nowadays. Some of the rarer newts repay care when bred in captivity. I am not certain that the reproduction of bullfrogs in ponds is a commercial proposition, or whether the so-called frog farms are not really devices to earn easy money from the unwary enthusiast. The same is true of alligator farms. It is hardly believable that it would pay to raise baby alligators to big ones and buy the food, all for the sake of the hides, an industry that would have to compete with the alligator hunters, whose standard of living is hardly a high one.

Terrapin farming is a different proposition because of the good price paid for the adults, and the fertility of these reptiles. It is probable that selection after crossing would be effective in improving the growth and the fertility of these animals.

With the present fancy for aquaria, the cultivation of newly-imported species of small fish has become an important industry, especially around Hamburg. Success is generally dependent upon finding the most suitable methods of feeding, the best temperature and depth of water. Both in the platyfish, and in the genus Lebistes, species-crosses and crosses between local species have been instrumental in producing a very great variability and many sometimes very striking varieties. Much more can be done in this field.

Laboratory Animals. For bacteriological, physiological and endocrinological investigations it is necessary to use a great many small animals. The usual system of procuring these animals is for the laboratories to parasitize upon the local fanciers, upon children who keep a few mice for pets and upon show breeders of guinea-pigs and rabbits. It rarely pays to breed mice or rats or guinea-pigs for the laboratories, for they are mostly sold below the price of production, simply because it so often happens that a child must try to get rid of a large colony of mice that have suddenly grown out of a few pets.

This system of utilizing just any sort of mice or rats is very bad for the work in hand. From our own investigations on disease-resistance in mice and food requirements in rats, it can be seen that in mice some strains are perfectly immune to infections that quickly kill off the animals of different strains. In rats some strains need far more of certain vitamins to stay in good health than other strains, and as rats are very often utilized for experiments on vitamins, it is evident that some of the results,

based upon the behaviour of just any rats, are built upon sand.

Sewall Wright, working for the American Government, showed that different strains of long in-bred guinea-pigs differ considerably in such important qualities as resistance to tuberculosis and as one of the most common uses to which these animals are put is to test the presence of tuberculosis bacilli, the breeding of specially susceptible strains is highly desirable to speed up such tests.

We have investigated the possibility of making the breeding of small laboratory animals pay, as this would be the first thing to know before recommending the establishment of special in-bred lines to breeders. At present it hardly pays to breed these animals; but it will certainly be necessary to produce specially selected and highly in-bred pure strains of laboratory animals, even if this work has to be subsidized. At present a number of highly in-bred and very pure breeds of rats and mice exist, and we made a few of these ourselves; but none of those lines has been selected for any definite bacteriological or physiological purpose, with the exception of one strain of white rats in the laboratory of Swift & Co. in Chicago.

With rabbits, laboratories should make use of the fact that show fanciers have produced highly in-bred strains of rabbits, and from among those breeds they should select a breed suitable for their purpose. It would cost too much to breed their own strain of rabbits, as most breeders sell their stock below cost of production.

The best way to produce pure in-bred strains of small laboratory animals, as I know from experience, is to keep a few parallel lines, scrapping most of them when one has proved sufficiently viable, and then split this line into two or three separate parallel lines again and so on. If we just simply keep the first litter from a pair, kill off the parents, breed the litter and repeat, the chances are that we will get a strain with some defect which we have not guarded against. The animals may develop some abnormality rather early in life, or they may be extremely short-lived, or very infertile. By keeping parallel lines we may guard against this possibility.

After ten generations of in-breeding most of the genetic variability has disappeared from a line of rats or mice. After this the strain is in-breeding-resistant, and nothing can happen to it any

more. Some strains of mice and rats have been in-bred full brother with full sister for fifty and many more generations.

The Duck. Ducks are among the oldest of domestic animals. Very many breeds of these birds are in existence, some of them beautifully adapted to very peculiar circumstances. In another chapter I have mentioned the North Holland night-feeding ducks, and also the curious Javanese runner ducks.

Especially in France, first-generation hybrids between domestic ducks and Muscovy drakes are yearly produced in enormous numbers for table purposes.

Very few show breeds of ducks have been developed. The most curious one is the crested duck, with an enormous cranial hernia covered with feathers. Such crested ducks never breed true; they are always heterozygous for the factor necessary for a complete skull; and the recessive birds, that lack this factor completely, have a head that is so grossly deformed that the chicks cannot even break the shell. In poultry in a parallel case it has been found possible to produce true-breeding breeds of birds with cranial hernia and crests, and the same would probably be true in ducks if somebody took the trouble to try out this genetic aberration in different breeds by means of cross-breeding.

Species-hybrids between domestic ducks and related species such as the pintail and the shoveller are fully fertile. Darwin's idea that the domestic ducks originated from one parental species is probably not true.

Special breeds of table ducks, such as the French Rouen, the English Aylesbury and the Chinese Pekin have been established, and several special breeds for egg-production have become known. Elsewhere I have described the curious case of the Khaki Campbell duck, originated as a show bird pure and simple, which happened to have a better egg-laying quality than any of the other breeds. Just as in poultry no special breed of laying-duck has been deliberately made so far.

In Holland the duck-egg farmers have almost from the beginning adopted a rational system of progeny-tests for the selection of their stock. This system, first advocated by me for poultry, adapts itself extremely well to the local system of keeping ducks in small flocks, but in enormous numbers. On the mammoth duck farms it is now the rule to keep those groups of ducks for breeding stock, which as a group have shown to be the best,

most profitable groups. As these groups are each composed of the daughters of one father, this means a straight progeny-test in the male line. No individuals from mediocre groups are ever used for breeding, no matter if they are individually excellent. This is an almost perfect system of selection according to genotype, that could with great profit be copied by breeders of cattle or swine.

One of the foremost breeders in Holland, Mr. A. Jansen, has in a few years succeeded in raising the average production of his whole farm of about 50,000 ducks from an average of about 240 eggs to over 300 eggs per duck per annum (350 in 1953).

Laying-tests for ducks differ very much from country to country. The English tests make the great mistake of preferring large eggs to cheap eggs, and of requiring certain marks of beauty in the birds. The best regulations are those of the German egg-laying tests for ducks, as here the group is preferred that has given the greatest profit out of the value of the eggs produced with the cost of the food subtracted. The value of ducks as egg producers lies in the fact that they produce protein cheaper than hens. Laying ducks will never become popular or profitable in England until the laying-tests are so managed that in every instance the best, most profitable pen wins the tests over the less profitable birds, whether they have white in the neck or not.

The Goose. Geese are not generally kept in great numbers by individual breeders; they are mostly in the hands of small owners, each of whom keeps a few birds. This does not make for conscious selection, but it makes possible a selection between the small groups. The groups that are kept profitably, because they are adapted to local conditions, tend to get larger, and unprofitable groups tend to disappear. The goose is not quite monogamous, but sufficiently so during the breeding season to make the goose population propagate itself as a multitude of parallel lines, practically isolated one from the other. Many local breeds exist, but the differences are not very large.

Where geese are wanted, the best thing is to try out a number of local groups, and when a profitable group is found, to keep it free from cross-breeding. Some groups are very much more fertile than others and especially in the northern countries growth in the goslings is surprisingly rapid. In special circumstances, first-generation hybrids, especially species-hybrids, are

raised for market. In America and Canada hybrids between the Canada goose and the domestic goose sometimes command a very special price in some markets. The hybrids of which one parent is a Chinese goose are very strong and quick-maturing. These last hybrids are perfectly fertile, and from these hybrids a very variable population can be bred in which it would probably be possible to find material for the making of novel breeds if such were wanted. Whether a few very large or many very small geese are more profitable depends upon the demands of the market; possibly on very poor pasture small geese would be at an advantage. The shows have made very large geese fashionable. It is certain that one large goose is more valuable than one small one, but probably the two small ones could be kept on an area only sufficient for one large one and together they would be worth more money.

In certain localities very striking characters are sometimes seen in geese, such as extremely long feathers, and topknots. Such characters could easily be made to serve as trademarks by which to recognize a definite new breed, but I doubt whether it would really ever pay to go to the trouble of deliberately producing a new breed.

The Turkey. Turkeys, up to some years ago, have always been bred extensively, a few here, a few there. To-day large turkey farms exist. The existing races have originated as land-races, never as the result of deliberate experiments, or in order to fulfil a special need.

The result is that the turkey consists of a multitude of small local races; there are probably as many breeds of turkeys as breeds of chickens. While local breeds of chickens have disappeared in competition with internationally-known breeds, this has seldom happened in the turkey. Another result has been that turkeys have special qualities that make it difficult to herd them together in large numbers. The main difficulty is their susceptibility to disease.

The breeds of turkeys differ mostly in colour (wild-grey, black, white, blue, buff, yellow, silvered (*Narrangansett*)), in size (from the enormous Mammoth Bronze to the small Black French breeds), and in tameness (from the wild American ones to the tame small French).

The main turkey breeder's problems centre around disease-

resistance. Bringing turkeys to new, uninfected pastures is no final remedy. The best thing to do is to study the birds in countries where they have been raised on the same ground continuously (France, Italy) as here the possibility is greatest that naturally-resistant strains will be found. Probably cross-breeding and selection is another good method to obtain variability in resistance, and a good basis for selection. This work is too difficult to be undertaken by any private breeder—it is experiment station work.

Turkeys differ enormously in the amount of food consumed for every pound of gain, and it would be very much worth while to select for economic food consumption in a variable flock.

The correct method to use would be a method of progeny-testing, in which lots of descendants of individual fathers were compared, and in which the group that averaged best in different ways would be chosen to continue the breed. Trap-nesting is possible but does no good here!

The first step in obtaining a breed of turkeys that is well adapted to particular conditions should always be to try a number of existing pure breeds, even if this means introduction of new breeding stock. It would be manifestly absurd to spend time and money in creating a breed that already exists somewhere else. Experiment stations can do extremely useful work along these lines.

In turkeys, as in poultry, first crosses are sometimes much preferable to either parent breed, and, as in poultry, this points to the presence of many recessive lethals in different strains.

Where a good combination of two breeds is discovered, in which the eggs hatch very well and in which the chicks grow quickly, this combination should be remembered, and made over and over again. Breeding from such hybrids, however, no matter how good they may appear, should be discouraged, as it would only mean a heaping up of recessive lethals in the family.

For the same reason, selection for growth-ability should never be based on the individual value of separate birds, as very good birds from lots of mediocre average value should be avoided. The correct procedure is to base selection on the average value of whole groups of birds of common parentage, and this is only another way of saying that progeny-tests in the male line should be used as a basis for selection.

In Russia, experiments with artificial insemination of turkey

hens with sperm of the domestic cock have resulted in several hybrid embryos. Artificial insemination would be a very successful method of mating turkeys, especially when breeding from small or young females and using a heavy stag. The extra trouble entailed in gathering the sperm and injecting it into the oviduct of the hens would be more than offset against the injury a heavy stag can do to smallish hens in treading.

When a suitable breed is found that fits local conditions of raising and also the local market, in-breeding should be employed to keep the breed as pure as possible, and to purify it further.

Very few people have done serious breeding work with turkeys, and this bird offers a very good opportunity to the enterprising experiment station or large individual breeder. Where local conditions make it safe and profitable to let the turkeys forage, it would be worth while improving some of the smaller, more fertile breeds in regard to economic egg production. A strain of small turkeys, producing about 150 eggs yearly with a minimum of food besides what they can gather themselves, ought to be very profitable.

Pigeons. Most breeds of pigeons are only bred for the shows, and almost all the utility breeds are also shown—and this circumstance has its very peculiar influence on such breeds. A third category might be called "sporting breeds", which, where shown, also undergo the influence of the shows.

In different countries are kept pigeons that have to find their own food. The large pigeon-cotes and pigeon-towers that used to be kept fully populated on some of the large estates in Holland are now almost wholly out of use, because the tenants disliked having their landlord's pigeons in their seeded fields. This is true also for England. In other countries such large pigeon-towers still exist. The few flocks of these pigeons that are left in Holland, as at the castle of Doorn, and on some farms in Friesland, almost always consist of dark-blue checkered small pigeons, extremely quick in flight and very active on the ground. Such flocks are generally kept down by predatory birds in winter, and with the exception of a few squabs, their chief value used to be the manure they produced in the towers. In Oriental countries large flocks of cote pigeons are still kept.

The special table pigeons are almost all of French origin, in-

cluding the Carneau and the Mondain. The King is an American squab-producing breed, an improved, large bird of the Homer type. Good squab-breeds are very prolific, and the nestlings grow very quickly. As pigeons produce for several years, a system of individual selection that keeps the prolific pairs and weeds out the poor pairs improves the value of a flock. This does not mean that this would be a promising system of selection likely to improve the breed. As in all pigeons, in-breeding combined with a system of testing parallel lines is the best system of selection in these monogamous birds.

Homing pigeons are the chief sporting breeds. Most strains of homers nowadays are very strictly in-bred. It is probable that some improvement is still to be obtained by crossing different strains or even different breeds, followed by a system of inbreeding in many parallel lines. The racing of pigeons is in itself a system of very rigorous mass selection, weaklings or birds without sufficiently developed homing instinct being automatically weeded out of the flocks of the competing breeders. Lethal factors are very rare in these breeds. We found one recessive lethal, complete blindness, in homing pigeons being inherited as a monofactorial recessive, the heterozygotes being good flyers and quite normal.

One of the Dutch amateurs bred a few first-generation hybrids between the stockdove (*Columba Ænas*) and homing pigeons, and those hybrids had a strong homing instinct and returned home from Bordeaux, France, to Dordrecht, Holland. The males in these hybrids are fertile when fed enough cod liver oil, so that one might try to improve homers by introducing a few genes from this cross. It is quite possible that other fast-flying breeds could be used in this way. Whereas the Carrier has been "improved" so much for the shows that it cannot be considered as a real homing pigeon, it is quite thinkable that even a more rapid bird than our present best homers could be constructed from a novel combination of genes present in the homer plus the carrier, by means of hybridization and selection from the second generation on. It would serve no useful purpose to expose the first-generation hybrids to severe tests.

Homing pigeons furnish an extreme example of what happens when the shows have an influence on a breed that is also used for some different purpose. Long ago the show homer was split off as an offshoot of the flying breed, because at the shows judges

gave attention to special external characters. When the show homer was visibly distinct from the flying homer, the flying homer was again sent to the shows. The result of this was, of course, that a second time a show bird was split off from the main stem, mostly because of the fact that fanciers crossed in other breeds to "improve the type" of the flyers. This process was repeated once more, until to-day at the pigeon shows of Holland and Belgium we see special classes for show homers, for exhibition homers (beauty type), for homers (flying type), and lastly real flyers with flying records. I see no reason why this process should not go on and give us nine or ten different show breeds, all split off from the main stem.

The other sporting breeds are mostly performing pigeons, tumblers, rollers and tipplers. Most of these pigeon breeds are very closely in-bred, and the genetic variability is probably very slight in each breed, so that the difference in duration of flight between two kits of tipplers is very probably mostly due to a more or less suitable system of handling, training and feeding the birds, and assembling the kits.

It would be rather difficult to improve such breeds, although it is quite possible that cross-breeding might be used. This means that it might be possible to obtain an improvement by mating hybrids, e.g. between tipplers and one of the Continental breeds of high-flyers, back and back to the parent breed. Breeders trying such experiments should not be discouraged if the original hybrids are rather poor, as an ultimate good result does not depend upon their quality.

Curiously enough, even the breeders of such birds as tipplers and rollers cannot be satisfied until their birds compete with each other at the shows, merely on beauty points.

The inevitable result of showing performing breeds is that their ability to perform deteriorates. This is not simply due to lack of selection, but mostly to hybridization. A tumbler is mated with some other pigeon to make the beak longer (or shorter, as the case may be), and hybrids are bred back into the breed to improve it for show purposes. As the typical behaviour of the birds cannot be judged at the show, less extremely-shaped wonderful performers have no advantage over bad performers with the show points developed to perfection, and the result is always the same, we get performing strains and show strains.

Breeding pigeons for the shows is a fascinating hobby. Selec-

tion combined with in-breeding is the correct system in all breeds, until the genetic variability drops so low that no further progress is possible. At this point cross-breeding often comes in useful, especially where the judges are looking for extremes. Elsewhere I have given a few examples of this. Progress is most rapid when there are produced hybrids that excel in some special point, in which case repeated back-crosses can be used to incorporate this point into the breed. Sometimes striking novel breeds may result as a by-product of this process—such as the Matram from the making of the improved Magpie.

Wholly new breeds can still be made by the dozen in pigeons, by combining the striking colour of one breed with the striking shape of another. The relatively small fertility of the pigeon does not favour this process, but with perseverance it can be done. The best way here, as in all such instances, is the introduction of one gene into an existing breed.

Cagebirds. The canary is the most popular cagebird. Several wild birds are related to it. The tame canary, as we know it to-day, probably originated from fertile species-hybrids. Canaries have been utilized for genetic experiments by several geneticists, although they have several drawbacks for this work. The most difficult thing to breed for is song, as this can only be judged in one sex. In-breeding is the only correct system of breeding, and when a breeder deems it advisable to use an outcross, repeated back-crosses to the pure strain should be resorted to before the new "blood" is used at all freely in a strain.

The most interesting work in canary breeding is cross-breeding with different species. The most common hybrids are canary-goldfinch, canary-siskin and canary-redpoll hybrids. Most of these hybrids are sterile. Breeders always aim at producing "light" mules. The amount of yellow on the hybrid is mainly due to the genotype of the canary. It is a mistake to think that all-yellow canary hens are best for this purpose. Special strains of canaries, which have been selected from females that produced very "clear" mules with goldfinches, used to be kept pure in some parts of England. This is a sensible way of doing this work.

Siskin-canary hybrid cocks are not always completely sterile. It seems that in a large aviary these cocks sometimes become fertile after a few years. So far I have not been able to corroborate

this from personal experience, but I do not doubt the truth of the statement.

The orange-red black-headed siskin produces fully fertile mules with the canary. These hybrids have been bred back with canaries, and strains of orange-coloured canaries have been so obtained. Breeding those birds back once more to the wild species would certainly give us blood-red canaries in time.

The Japanese have produced the white paddybird. It is not known what cross was originally used to make the paddybird variable, but it is not probable that the white is just a white "mutant" of the Javanese grey species, as whites are true domestic birds that can be bred in small cages, and the young raised by hand on a mixture of rice and fish. The grey species does not readily breed in cages or aviaries.

The Japanese have given us another true domestic bird in the little Bengalese. These little birds are bred in several colours; it is not known what species-cross gave rise to them, but probably some nuns are related to them. It would certainly be worth while to try to repeat the process, both in this same group and in other groups of cagebirds. This is especially true in such groups as that of Mrs. Gould's finches, beautiful and expensive birds, well worth the trouble to breed. Cross-breeding between closely related finches might give us the variability required to produce true domestic breeds in this group.

Aviary Birds. Just as with fur animals, the breeders of aviary birds are mainly concerned with domestication. In this section I want to say a few words on the breeding of pheasants and breeders of other aviary birds will find that their problems are on the whole very similar.

It is a debatable question whether such birds as the Golden Pheasant and the Silver Pheasant are domestic animals or wild birds bred in captivity. If we use the definition that domestic animals differ from their wild relatives in being adapted to life under domestication by genotypic change, such pheasants are certainly domestic breeds.

It is very significant that in the three groups of domestic pheasants—the Ringneck Mongolian, the Golden Amherst and the Silver Pheasant groups—different closely-related species have been crossed from the very beginning. We know that hybrids are very variable in all respects, and the domestication

of those pheasants is surely due to selection from hybrid populations of the groups best adapted to cage life. Breeders who want to make use of what we now know about these matters could easily duplicate this process deliberately in other groups, such as the Trapogans. In those three hybridized groups there have originated varieties, albinos, dark goldens, Picta-Amhersts, etc. The same thing would surely also take place in other cases where the breeders bred on from species-hybrids. I am thinking especially of species-hybrids in peacocks, and in guinea-fowl, which are generally fertile in those groups. I would be extremely surprised if hybrids between different species of peafowl, when bred together, did not produce such novelties as buffs or blacks, and it would certainly pay anyone able to keep such birds to try this.

In the ringneck group, where birds are wanted for shooting, pheasant-farms would be well advised to try cross-breeding experiments with the object of selecting for disease-resistance.

Very little work has been done so far with aviary birds. Breeders should be on the look-out for groups of species that will produce fertile hybrids. Doves and pigeons, which hybridize freely but give sterile hybrids, are not promising, but in the parrakeets, e.g. in the Rosella group of species, very profitable breeding work could be done.

In budgerigars most novelties have originated through mutation. Novel colours are sure to crop up occasionally, and it pays to look out for them. In this respect it pays very well to be on the lookout for birds with stray feathers of an aberrant colour. I know of one instance in which albino budgerigars were located in this way and produced from heterozygotes afterwards.

Breeders of these birds should remember that what they consider ugly in a novelty may be thought beautiful when birds of the new colour are rare enough. Greywings were often produced in Holland years before the variety was recognized, and such aberrantly-coloured birds were not regarded favourably. The same thing is true of black-headed budgerigars to-day. A little judicious advertising would make those unwanted aberrant "sports" worth money.

The Ostrich. Ostrich breeding has experienced a period of depression caused by the circumstance that the feathers have gone out of fashion. It seems as if the cultivation of ostriches will

become profitable anew. This domestic bird, like the guinea-fowl, hardly merits the name, for it can hardly be said that the cultivated birds differ from wild stock in qualities that make them better adapted to cultivation. This is probably due to the fact that most ostriches are derived from one wild species.

From what we know in other animals and birds, it is very probable that in the ostrich the hybridization of species would produce some variability, and that this variability could be utilized in making breeds that were better adapted to cultivation. The blue-legged Somali ostrich has been mated in zoological gardens to the commoner pink-legged ostrich, and it is probable that this cross will be of great value in the above-named respect.

One of the most important qualities that need improvement in the ostrich is the bird's food requirement. Most domestic animals and birds differ from their wild relatives in that they can be fed more cheaply and that they will be more profitable on the same amount and the same quality of food. The fragility of the legs in mature chicks might be very much less serious if the birds had been selected with an eye to paddock feeding from variable material, and the same is true of hatchability. Species-crossing should be recommended in the ostrich as in all other domestic animals of monophyletic descent.

Food-Fishes. The chief groups of fish cultivated for the market are the carp, with the goldfish, the trout and, in the Tropics, the gurami. The cultivation of fry for releasing, or the reverse process, the raising of young seafish in ponds along the seashore, we will leave out of consideration, as no continuous control of several generations is then possible, so that no real selection can be practised.

Trout, especially where cross-breeding between species and sub-species has been practised, vary enormously in quickness of growth. When from a pond the largest fishes out of each lot are continuously caught for market and the smaller ones kept, this means contra-selection, if some of the laggards are eventually used for breeding. On the contrary, a trout-breeder should make it his practice to keep for breeding stock the fish that mature most quickly. Most large trout-breeding plants use artificial insemination and hatching in trays. This gives complete control of the breeding. It will pay to keep booked account

of the ultimate fate of each lot, so that profitable, quick-growing, healthy batches can be utilized for breeding stock. With the enormous fertility of these fish, selection can be very strict indeed, a few individuals sufficing for raising the next generation. Breeders should not make the mistake of relying only on the selection of fish of individual excellence; the excellent ones out of a very mediocre batch should never be used.

Goldfish and carp are generally left to mate naturally in smaller ponds in groups. Wherever possible this should be changed to mating pairs, because this makes selection more effective. Some of the breeds of carp are much more fertile than others. Goldfish differ enormously in growth-rate; some of the Javanese goldfish can be raised to a desirable size for frying in a very short time, so that they can be grown as a secondary crop in the inundated paddyfields where conditions of temperature, water-supply and insect life are favourable. Colour is of some importance in goldfish for eating purposes; the carp-coloured fish, such as those that have run wild around the American state capital, would be undesirable in this respect in countries where goldfish are eaten in large quantities.

The gurami is a doubtful animal on a list of domestic species, but it has been raised generation after generation in large ponds in many islands of the Malayan Archipelago. It is evident that the same principles apply here as in the other food-fish.

The Honey-Bee. The honey-bee, owing to its peculiar ways of breeding, has a unique position in animal breeding. As females, queens and workers develop from fertilized eggs, and drones from unfertilized haploid eggs, drones have daughters but no sons, and they have no father, but only a maternal grandfather.

It is very difficult to control matings, and so far no workable method has been found of mating a queen to a certain drone in an enclosure. It has been found possible to establish mating stations, which have been freed from undesirable drones. Islands are especially useful in this respect, as has been shown in Holland and in America.

Methods of artificial insemination have been tried repeatedly. At present two workable methods are being used, the Quinn-Laidlaw method of hand-mating, and the Watson method of artificial insemination.

In the former method, the queen is held fixed in a glass tube, and the drone is held in such a way that its genital organs are partially everted. It is then so placed that insemination of the queen takes place when eversion is complete. In the Watson method a syringe is used, by means of which the sperm from a killed drone is transferred to the queen's receptaculum. It can be diluted with a salt solution.

The sperm remains alive for several years, and it can even be taken from the receptaculum of one queen and transferred to another one, which makes it possible to produce back-matings to males that have been dead for a long time.

It has been shown that several economically-important qualities in the honey-bee—gentleness, use of propolis, tendency to excessive swarming, etc.—are mainly determined by heredity, and can be re-combined in the most desirable combinations. Bee breeders are very fortunate in that it is possible to breed several generations a year by means of artificial methods.

The work of the American Department of Agriculture is of the very greatest importance in this field, and very great progress can be confidently expected from this work in a few years. It has repeatedly been shown that the most serious disease bee-keepers have to contend with (foulbrood) does not attack all colonies when an outbreak occurs, so that it seems possible to establish disease-resistant strains.

As with all other animals, the breeding of honey-bees will have to pass through a stage in which progress is sought by means of cross-breeding and re-combination of analysed genes. Finally, the breeders will have to resort to selection according to genotype to fix the breeds. In the honey-bee a very peculiar state of things is caused by the fact that the queen is not productive in herself, and that the only character we can estimate in a queen is fertility. The qualities sought in bees can only be determined by a comparison of colonies, and as each colony consists of the daughters of one mother, the ordinary selection in bees is really a selection according to genotype, testing for quality here meaning progeny-testing. This fact ought to make selection in cross-bred groups of honey-bees very effective.

The Silkworm. A great amount of work has been done on the genetics of the silkworm, on colour, silk colour, difference between univoltine and multivoltine breeds, etc. The great fer-

tility of the moths has made it possible to concentrate the production of eggs for the silk industry in special breeding stations, where bacteriological tests can be applied to the eggs distributed, so that the dreaded "flâcherie" can be kept in check.

Where the growing season of the mulberry is long enough, bivoltine breeds can be grown; in colder latitudes we must be content with univoltine breeds, which give one crop of larvæ in the season.

When starting the breeding of silkworms, we can either just import a ready-made breed or a great number of them to choose from, or we may make a new local breed adapted to local conditions from hybrid stock. The latter course could not be counselled to private breeders, but wherever experiment stations have been founded for this industry this is the way the work should start.

Different breeds differ considerably in rate of growth, in the final size of the larvæ, in quality of silk, in quantity of silk per cocoon.

Although it seems as if a rapidly-growing strain would always be preferable, as rapid growth produces a saving of labour, other factors are of equal importance. The best strains are those that produce excellent, marketable silk most cheaply. Whether the strain that produces the greatest amount of silk for a given quantity of leaves is the most profitable one depends upon the price of labour. Where the cost of labour is negligible, as in countries where the production of silk is a home industry, and where most of the labour is performed by children, the strain that gives the best production of silk for a given weight of leaves is the best one. In other localities a somewhat smaller, quicker-maturing breed, that would require fewer hours of labour per pound of silk, might be more profitable.

Where selection is necessary, this selection should be based upon the quantity and quality of the silk produced by the larvæ from one pair of moths. Mass selection of good-looking cocoons is unreliable, and might lead to the production of strains with undesirable qualities.

Pupæ should be kept in separate receptacles, and pairs of moths should be mated soon after their emergence. The eggs of each mating should be kept and hatched separately and the larvæ fed separately. Where in-breeding is practised, many different pairs of a brother and sister each should be handled in

parallel series, so that the most promising lines can be kept, and those with lethals and serious faults can be eliminated.

Cross-breeding and selection in silkworms, to produce profitable strains yielding the right type of silk economically, should always be part of the programme of a Government or co-operative silk experiment station, even when a fairly good breed is now extensively used.

It is not excluded that, after crossing widely-different breeds, the variability would make it possible to find strains that would utilize a food-plant that could be produced more cheaply than the mulberry, an annual by preference. In any event, mulberry selection is as important as silkworm selection.

Chapter Forty-One

Australian Sheep and Cattle

A breed of domestic animals that has been bred and used in any country and that has been isolated there and protected from the introduction of foreign stock will gradually become adapted to the climatic and agricultural conditions of that country. This is generally a slow process under the older system of selection according to individual quality. It means that herds and flocks that happen to thrive will tend to expand and will gradually supplant groups that do less well. The adaptation is always of two kinds, an immediate, direct effect of the environment on the individuals, and the slower process of a change in the average constitution of the breed by conscious and unconscious selection.

The breeding of sheep and cattle in Australia furnishes excellent examples of the origin of local, well adapted breeds, and of the difference between such breeds and imported breeds that have never been completely isolated and freed from the effects of importation of breeding stock from the country of origin.

In sheep, the Merino and its derivatives, the Corriedale and the Polworth, are products of selection under Australian conditions. Of course even in these breeds the original material was imported. The Merinos, as they were originally imported from the Mediterranean regions, where climatic conditions were not greatly different from those in their novel surroundings, were modified by later importations and by crossbreeding with sheep of earlier importations, but after this they were evolved by a system of selection under local conditions of climate and handling.

From the beginning these wool sheep were split up into more or less isolated groups, and to a great extent the evolution of

our present Merino must have been due to a competition between groups that happened to be better or less well adapted to their use. Fundamentally, this process, the supplanting of less successful studs by better ones, is very much like our modern methods of group-selection, based upon progeny tests, with the difference that it tends to be economically wasteful. In this development of the Australian wool sheep, it has been of great importance that while it was going on, the groups were free of further importations. Adaptation to local conditions is a slow process, the qualities differentiating the better from the less well adapted groups are not easily appreciated, and while the group is gradually settling down and obtaining a set of genes which will make it fit better and better, introduction of livestock from elsewhere, especially stock adapted to wholly different conditions, would reintroduce heterozygosity and make the group more variable. And this is especially bad when such imported animals are looked upon as of special value.

This is just what is happening continually in the case of the so-called "British breeds". Here the parent studs are still in existence in their country of origin, and often enough exceptionally good-looking breeding stock is imported.

It is interesting to inquire into the reasons for such importations. We must remember that the climatic conditions, the rainfall, the mild winters, the abundant sunshine, all exert an immediate effect upon our animals. This will make the Australian-born sheep different from their close relatives born in England or Scotland. In the second place the tastes of the show judges may be changing. Lambs of the British breeds, imported as embryos and born in Australia, differ from the sheep imported as adults. In so far as the gradual change, the "coarsening" or "degeneration", or the legginess of the sheep in their new country are symptoms of a direct adaptation to the new conditions, the importation of even just a few goodlooking individuals in a breed, if these are given much prominence, will effectively hinder the process of adaptation which would go on without this. In such cases the show system with its artificial and false standards of value has an enormous influence. Such British breeds are adapted to climatic and agricultural conditions in their country of origin, and importation of "good" stock will make it more difficult, if not impossible to obtain a good fit of those breeds to a totally different country.

The Merino has been free of this danger for very many generations, and if the breeders of British breeds overseas could be induced to stop the importation of good-looking individuals, and concentrate upon the points of practical value this would be to their advantage. This would allow the breeds to adapt themselves to Australian agriculture. As the situation is today, not one of the "British" breeds is of any economic importance in Australia as such, their value lies in the utilization of rams in crossbreeding schemes. The Border Leicester is used to produce valuable crossbred ewes from Merino, and the Southdown as well as the Dorset rams give valuable fat lambs from those crossbreds.

Evidently, the system of selection indicated in the case of such breeds in Australia would be the progeny-testing of rams, using them as fathers of crossbreds, and giving preference to the proven good ones in continuing the breed. This might easily change the type, the conformation of those breeds, it might make the Southdown leggier, but it would certainly be more logical and practical than the present system of choosing such sires according to the dictates of the show judges.

The Merinos have been free from the danger of importation for very many generations, and the same thing is true in respect to the Corriedale and the Polworth. Those breeds are still rather variable, and this variability, due to the original crosses, has not disappeared as much as in the Merino. The methods of selection and of purification employed have been very little effective, probably partly for the reason that the standards of value have tended to vacillate in such dual-purpose breeds.

Several breeders of Corriedales have started progeny-testing and group isolation and four or five generations of this will assuredly make the breed more uniform.

It seems curious for an observer from overseas that in Australia the terms "imported" and "British" are used as synonyms in regard to sheep and cattle. It is understandable, but still remarkable, that all of the imported breeds of sheep and cattle are British, especially if we see that the one breed which is truly Australian and of the greatest economic importance, the Merino, was a typically Mediterranean breed. Spain and the South of France, regions where climatic and feeding conditions are much more like those in Australia, have many different excellent breeds of sheep and cattle, and I am

convinced that it would pay very well to import half a dozen breeds from this region for trial.

With the exception of the Illawarra Shorthorn all the cattle in Australia are of Northern European origin. And all those breeds suffer under the handicap that animals newly imported from Europe tend to have a very great influence as sires, which must stop the normal process of adaptation to Australian conditions from having its salutary effect on the breeds. In the long run this should be to the advantage of the one Australian breed.

In beef cattle, false standards of value at the shows are especially harmful. In Australia the Hereford's rôle in the economy of the country must be to furnish sires for the extensive system of breeding bullocks in the million-acre cattle stations where conditions are often very rough and where good mothering qualities are of enormous importance. It is manifestly absurd to see how often the young mature bulls that are still being suckled by Jersey nurse cows and that have had a supplementary diet of eggs carry away the blue riband at the shows.

The breeding methods of the big Australian sheepstuds happen to be of such a nature that they can readily be adapted to a nucleus system. In the first place the important studs are operated as closed flocks. The number of rams used per generation is so large, that within the stud the potential variability tends to remain at the same level. It seems that the stud breeders have all felt this to be so and they have almost in every case concentrated their chief efforts upon the improvement of a relatively small central or upper stud, which furnishes them with the rams of their main ram-producing flocks.

From this system to progeny-testing, and from progeny-testing to a nucleus-system in which only the sons of the father of the best group are used in the top stud and are tested in their turn, are only relatively small steps. In mating the spare nucleus rams to more general flocks, such studs still use what is mostly termed "corrective mating", joining the very strong-woolled ewes to fine-wool rams, and the overdeveloped to very plain-bodied rams. But the present generation of stud breeders are generally convinced that the result of such matings have only a very doubtful value as consistent breeding stock, no matter how good their individual qualities are or how big a price they bring at the sales.

The breeders using this system of group selection combined with mild inbreeding have the same experience, namely, that their culling percentage goes down. We still meet the occasional stud breeder who boasts of his heavy culling, but the idea that culling is an economic evil is winning ground, and buyers of rams are beginning to appreciate purity and lack of variation. The old practice of breeding specially mated selected rams for the shows and the sales and building them up by means of all the tricks of the trade is still going on, and both the selling and the buying of the three thousand guinea ram still has great advertising value, but the buyers certainly appreciate it when they find that a group of rams they bought give them uniformly good offspring.

At some of the studs a thousand to several thousands of ewes are individually mated every year for the progeny tests, and work of a high standard of quality is done at many studs.

The most common mistakes I met were those of promoting the first-class sons from a sire that on the whole disappointed, into the top stud, and a general fear of inbreeding that was holding down quick progress in some studs.

A number of Australian experimental stations are doing excellent work in the use and perfection of group-selection systems, both in sheep and in poultry, and many poultry breeders are beginning to obtain very good results.

I did not see as much of the Zebu crosses in Queensland as I would have liked. The idea of making such breeds as the Herefords variable by such a cross and of transferring the immunity of the hybrids into the pure breed by a series of repeated backcrosses is an excellent one. If it should be possible to avoid breeding from hybrid bulls this work would give excellent results, and I have the impression that it is in capable hands.

The existence of studs of polled beef Shorthorns and of polled Herefords in Australia is very promising. Such breeds should be protected from further importations now that the English herd-books are establishing sections for polled. Both breeds should now have a chance of working out a separate salvation, and of being adapted to Australian living conditions.

No specially Australian breeds of swine have ever been developed.

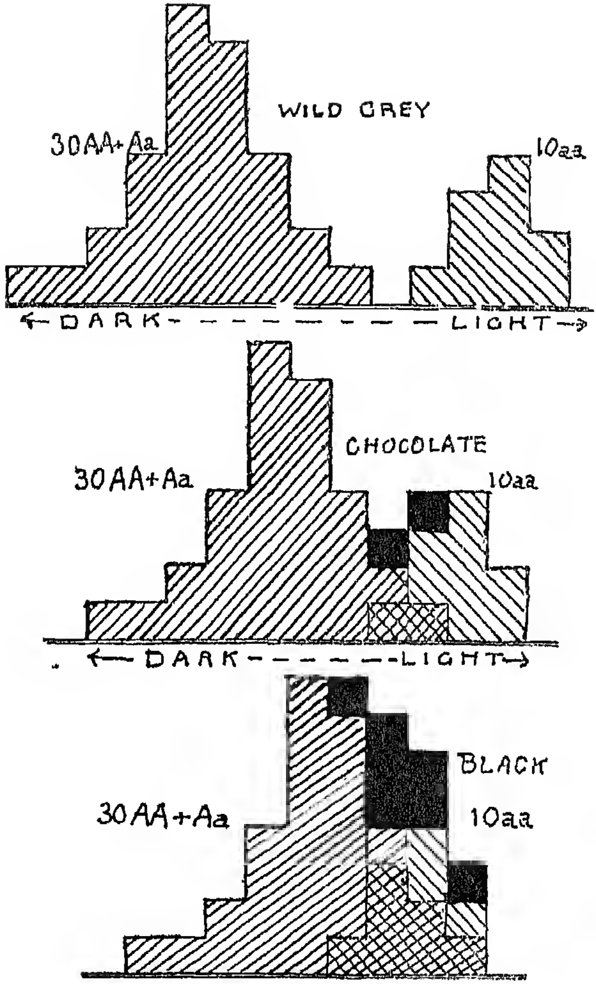


FIG. 38 (*see p.* 295).—Diagram to show the shape of variation curves in similar cases of a Mendelian 3 : 1 segregation in the offspring of heterozygotes. The gene for which the parents are heterozygous is the same in the three instances, but the rest of the genotype is different. Homozygotes and heterozygotes in respect to our gene tend to be darker than the recessives. A case of colour inheritance in mice is chosen. In wild grey animals the curves do not overlap, there is a clear case of dominance and of discontinuous variation. In chocolate animals we find a two-topped curve, and in black ones there is a case of continuous variation.

Two similar variation curves are drawn, 30 individuals with and 10 without the gene. The shape of the curve is obtained by moving the original ones closer and closer together. Where the curves overlap, the squares that belong to both sets (cross hatched) are added as black ones in the column in which they belong.

Redrawn from *The Relative Value of the Processes causing Evolution* (Hagedoorn & Hagedoorn, 1921).

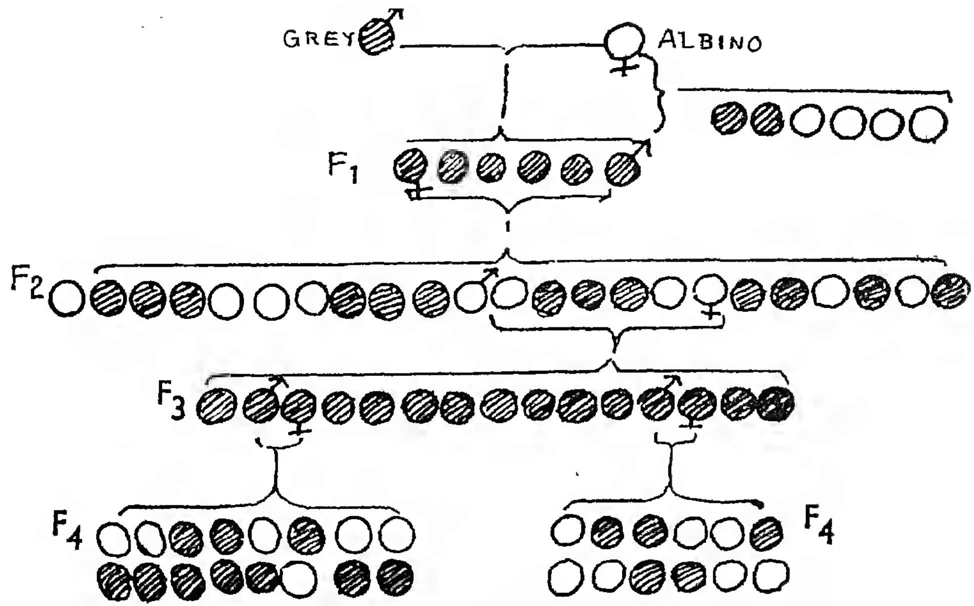


Fig. 39 (*see p.* 34).—Inheritance of albinism in Malayan field rats (*Epimys diardii*).

An albino "sport" caught on a Javanese sugar estate was mated to a wild field rat male from Sumatra. The hybrids were wild grey. One male was mated to his mother, and 23 F_2 animals were obtained. In both cases there were no excess of albinos (13 coloured to 10 albino in F_2). A pair of albino F_2 animals gave 14 wild coloured only, and 2 pairs from these gave 10 grey to 6 albino and 5 grey to 6 albino respectively.

All this can only be understood by the assumption that the original albino female was a *double recessive.*

Redrawn from *The Relative Value of the Processes causing Evolution* (Hagedoorn & Hagedoorn, 1921).

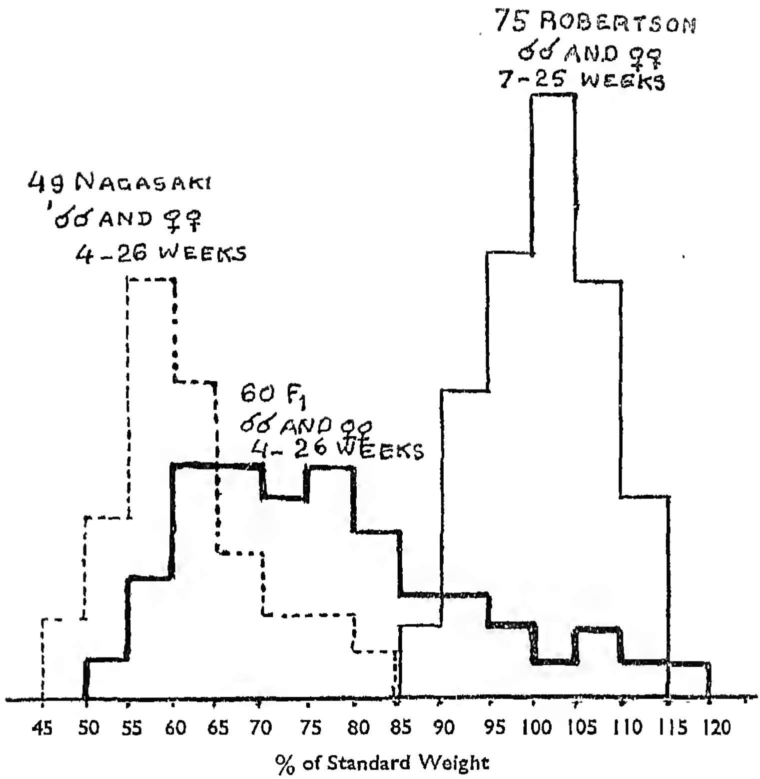


FIG. 40.—Inheritance of weight in mice. Two strains were crossed, a non-waltzing family of Japanese dwarfs, that we bought in Nagasaki during the first world war, Mus Wagneri, and the large albino Mus Musculus strain used by T. B. Robertson in his experiments on weight and age at the University of California.

To enable us to use males and females, and animals of slightly different ages, we expressed the weight of each mouse weighed in a percentage of the average (standard) weight of "Robertson" albinos of that particular sex and age.

The Robertson European albinos varied between 85 per cent. and 115 per cent., the top of the curve in animals grown in our mousery lying between 100 per cent. and 105 per cent.

The Japanese mice varied between 45 per cent. and 84 per cent. of standard weight, and the Nagasaki curve and the Robertson one did not overlap.

The first-generation hybrids were roughly intermediate in weight.

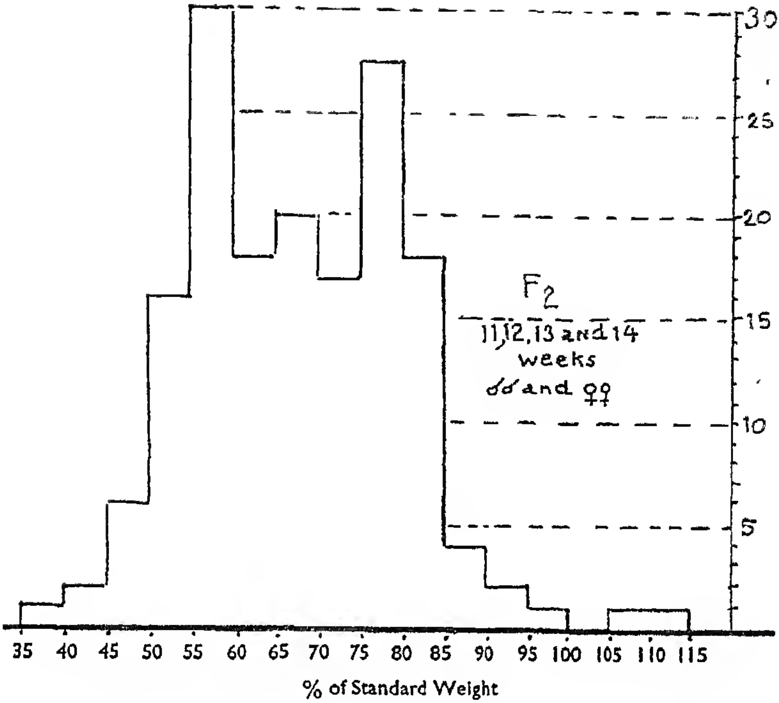


FIG. 41.—Inheritance of weight in mice.—Read with caption to preceding plate.

FIG. 42 (*overleaf*).—Inheritance of weight in mice.

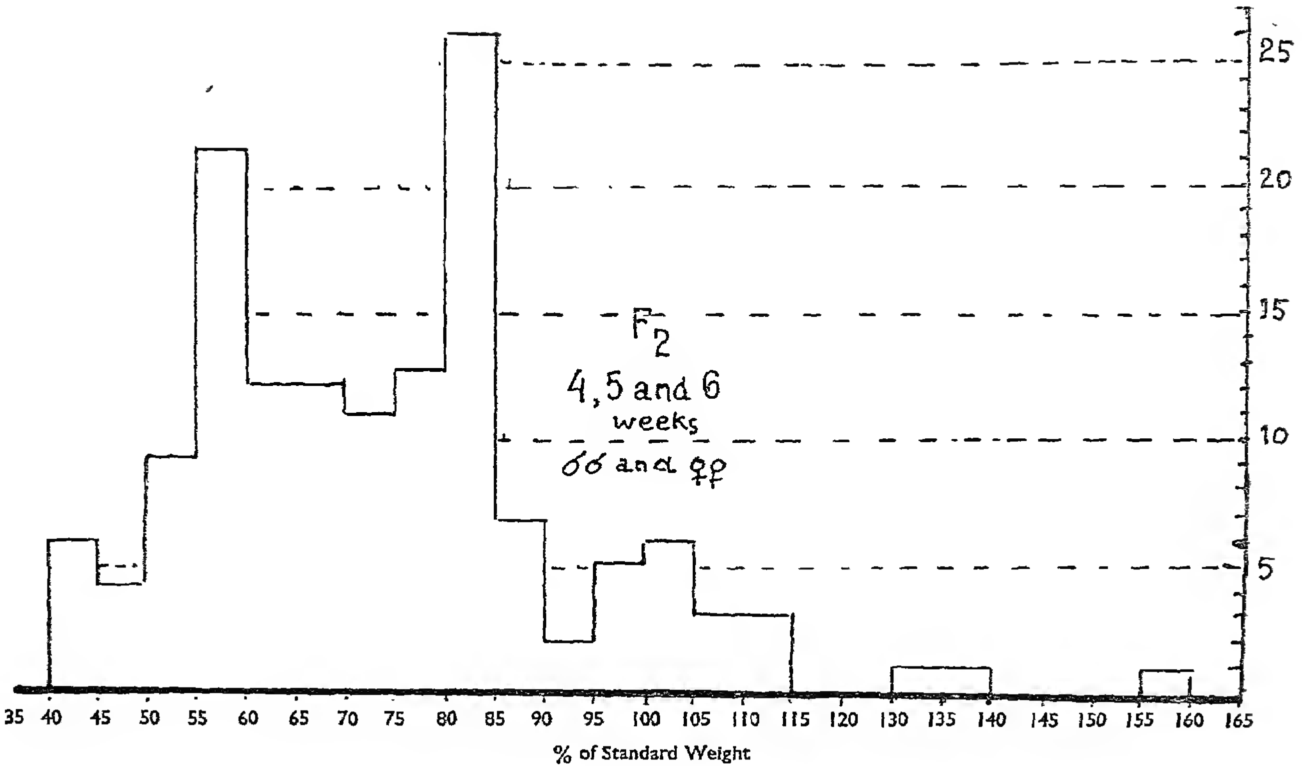
In the F_2 the variation curve, expressed in percentages of standard weight, decidedly showed two tops, one between 55 and 60 per cent. and another one between 80 per cent. and 85 per cent. when we compare young mice of 4, 5 and 6 weeks (of both sexes).

In comparing an F_2 population at a higher age, males and females at ages of 11 to 14 weeks old, with the variation in the same group when the mice were younger, we find that the tips of the curves are somewhat closer together, the heavier animals now falling between 75 per cent. and 80 per cent.

There is a very decided transgressive variation in the second generation, especially in the younger animal groups.

The whole mouse colony was fed on the same diet, and the temperature was kept as close to 25° C. as possible. Once a week a number of the inmates of as great a number of cages as possible were weighed.

The mice weighed were all weaned in small groups of one sex, and not yet used for breeding. The experiment was ended by an epidemic that in a few days killed off all the Japanese mice, a great many of the F_2 animals and many animals backcrossed to Nagasaki mice. (See "Inherited Predisposition for a Bacterial Disease", *American Naturalist*, 1921.)



25
20
15
10
5
F_2
4, 5 and 6
weeks
♂♂ and ♀♀
35 40 45 50 55 60 65 70 75 80 85 90 95 100 105 110 115 120 130 135 140 145 150 155 160 165
% of Standard Weight

FIG. 42.

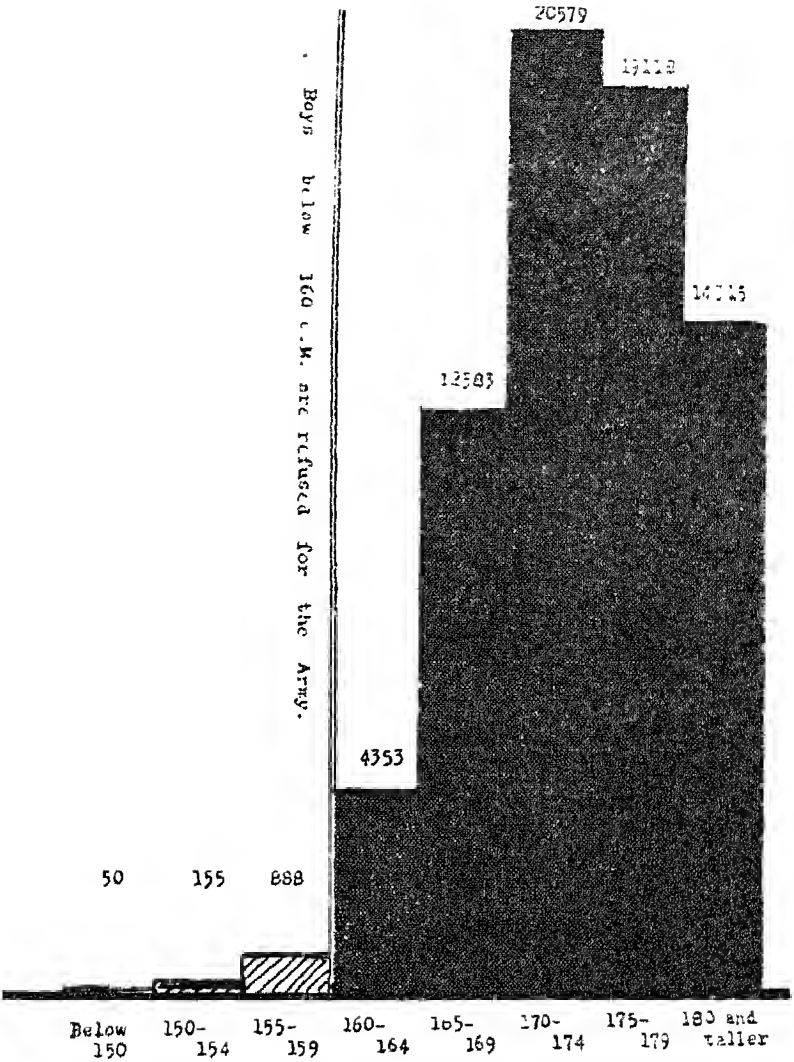


FIG. 5*a* (*revised*).—Height of the 71,841 boys in Holland conscripted.

Stature of the 71,841 conscripts in Holland in 1948. Boys below a minimum height of 160 cm. are refused. The boys are classed in eight groups. Attention is drawn to the fact that, in the lowest class taken, there are 4,353 boys, 6·1 per cent. of the total number, while 1,093 (1·5 per cent.) are refused. This bona fide variation curve should be compared to those of the heifers.

The three graphs 5a, b and c on succeeding pages replace those on p. 46. The latter were drawn on hypothetical bases, but the new ones are based on actual figures.

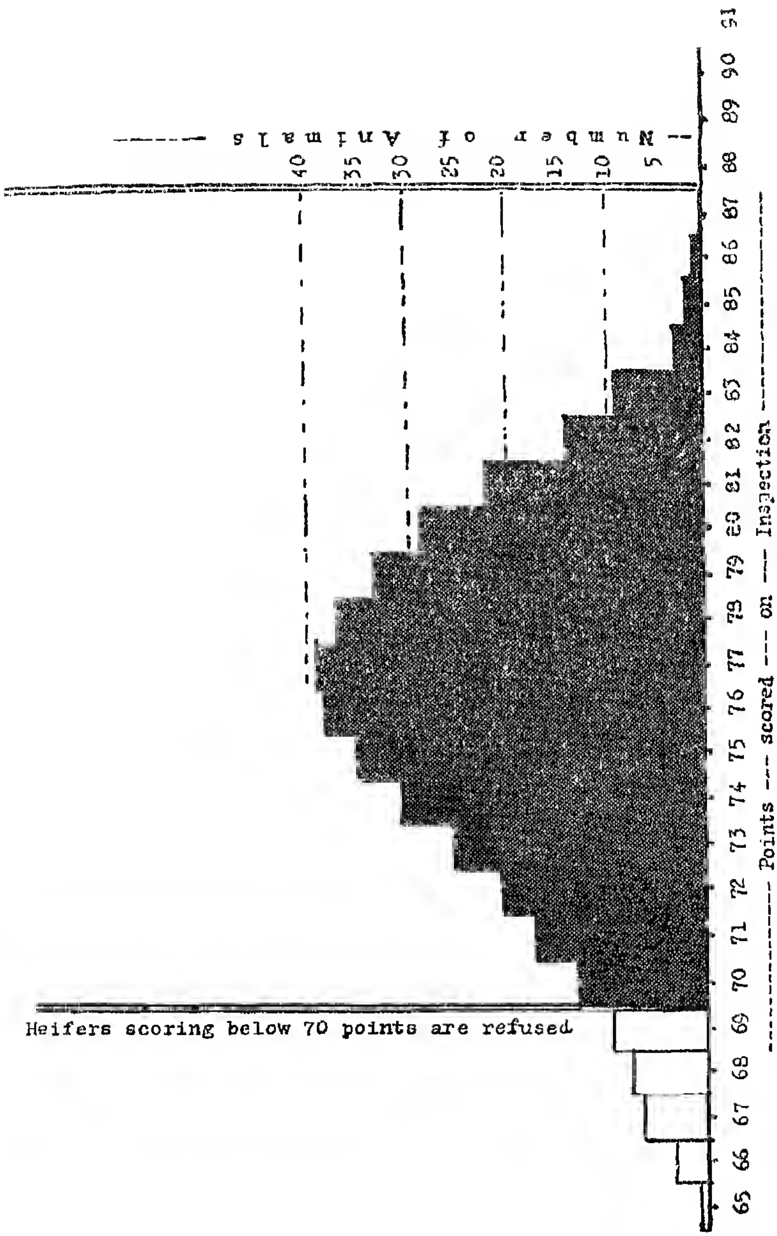


FIG. 5*b* (*revised*).—This is a purely hypothetical curve, showing how the variation might look if three hundred heifers were *really* selected from a sample, by rejecting those whose points did not add up to seventy.

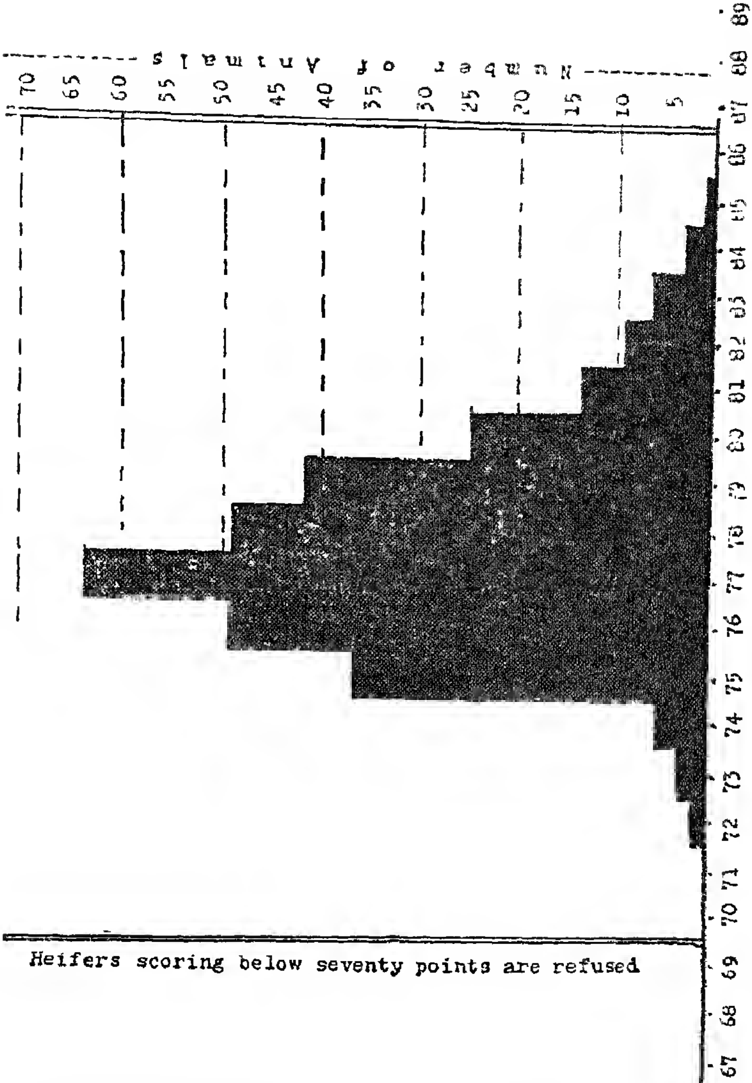


FIG. 5c (*revised*).—Three hundred young cows, consecutive numbers in the F.R.S. herdbook, operating in the province of Friesland, Holland.

The cows, on being definitely admitted, were judged according to an alleged scale of points, and the heifers whose points did not add up to seventy were refused entry. It must be remembered that the production during the first year is known when the judging starts.

The fact that among this group of young cows we find none who scored 70 or 71 points makes it probable (and this is what the judges tell us privately) that in reality the man scoring the beasts either likes the animal enough to take it, or does not like it and leaves it out, and that, more or less unconsciously, the points are juggled accordingly.

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